THE UNIVERSITY OF ALBERTA

STUDIES ON THE ECOLOGY OF MOSQUITOES IN THE BOREAL FOREST OF ALBERTA

by

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SUMMARY

The ecology of mosquitoes was studied during 1961 and 1962 in the boreal forest of Alberta, 100 miles north of Edmonton. Collections of larvae show that sedge and semi-permanent pools are the most productive habitats, and that larvae have a specific habitat distribution; transplant experiments show that this distribution is due to the behaviour of the female mosquito. The relationship between mosquitoes and other animals is discussed.

The fluctuations of the total adult population, and of *Aedes excrucians*, *A. punctor*, *A. riparius*, and *A. vexans* show many differences between the two years. Daily activity was studied, and the daily cyclical activity differs between species. Sampling at various heights in the forest showed that only three per cent of the population was found more than 15 feet above the ground. Biting activity is higher at ground level, and there is evidence that moonlight affects mosquito activity. Flight and biting vary in different habitats; of the 25 species recorded in the study area, two of them, *Aedes intrudens* and *Anopheles earlei*, form 80 per cent of mosquitoes found in buildings. The factors regulating mosquito activity are discussed, and it is shown that light intensity and saturation deficiency are the most important.

Keys to the larval and adult female mosquitoes, and a list of mammals, birds, and amphibians in the study area, are included.

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1. THE STUDY AREA

1.1 Introduction

The ecology of mosquitoes was studied during the summers of 1961 and 1962 near the southern limit of the boreal forest of central Alberta, 100 miles north of Edmonton (Fig. 1). The gently rolling countryside is crossed by several large rivers two of which, the Athabasca and the Pembina, join ten miles north of the study area. The village of Flatbush (54° 40' N. lat., 114° 10' W. long.) is two miles east of the Pembina River and seven miles northeast of the study area. The land between the two rivers is known locally as Athabina and is covered by forests of aspen and spruce, marshy swamps, and lakes. Homesteaders first arrived in 1928 and now some of the land is cultivated for crops and pasture. This varied habitat is rich in animal life; I saw 24 species of mammals and 107 species of birds during the two summers (Appendix 2). The number of animal species has probably increased as transitional environments appeared during the early settler days, but at the expense of some species which are now rare, *e.g.* moose. In the spring and autumn flocks of migrating ducks, geese, and cranes, as well as other smaller birds, pass through. It is difficult country to move about in since there are few roads, so the region for study was limited to an area approximately three miles by four miles between the two rivers from 54° 37' to 54° 42' N. lat., and from 114° 11' to 114° 18' W. long. (Fig. 2).

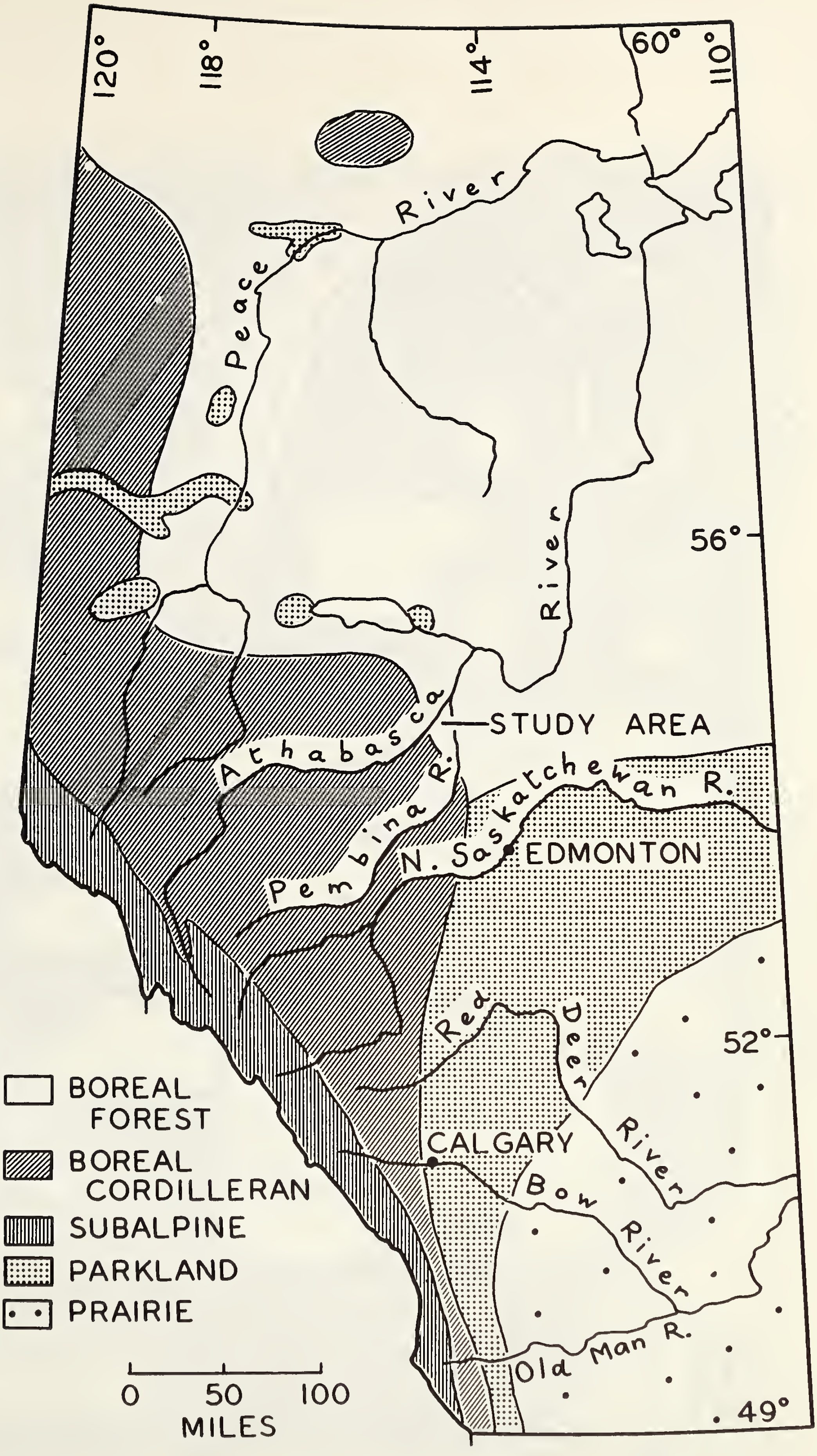

Fig. 1. Vegetational Map of Alberta showing position of study area.

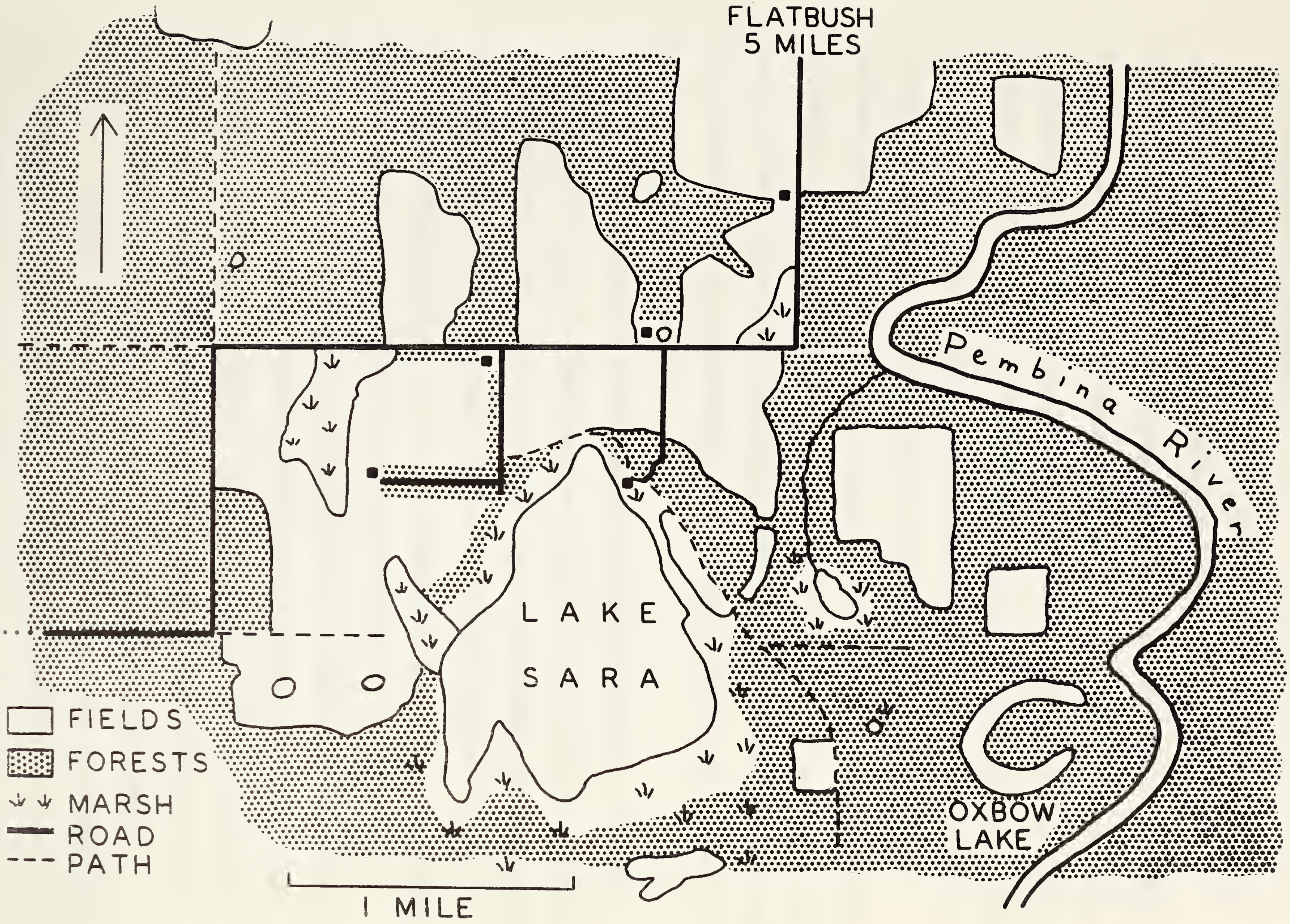

Fig. 2. Map of Study Area.

1.2 Climate and Weather

Central Alberta has a typical continental climate: summer is short and hot, winter is long and cold. From November to March, the ground is frozen and covered with snow. When the snow melts in March and April, the water forms many temporary pools which remain until June or July. The subsoil and deep waters remain cool until well on in the summer. There are two months or so between the snow melting and the trees coming into leaf. By the end of September all herbaceous vegetation has died and the leaves have fallen. Frosts occur in August and are common in September (Table 2). Most of the invertebrate life that flourishes during the brief summer months has disappeared by September, two months before the ground is blanketed in snow again.

Rainfall in the summer in Alberta differs greatly from place to place. The southern limit of the boreal forest rarely suffers from lack of rain. More important is the amount of snow during the previous winter which determines the soil moisture and the duration of the snow melt pools in the spring. Summer rains may increase the time that pools remain and so allow the later species of mosquitoes to complete their development, or they may reflood dry regions causing dormant eggs to hatch. Although rainfall will not affect the development of the early mosquito population, it may cause fluctuations of the population within a year, and from year to year.

Temperature and relative humidity were recorded during the summers of 1961 and 1962. A thermohygrograph was contained in a Stevenson screen, 36 inches above the ground, exposed to

the sun all day except in the early morning and late evening; the surrounding vegetation was low grass. Frequently a wind was blowing from the lake fifty yards away which probably raised the humidity readings above average. Although these records are of little value when discussing mosquito activity, they are useful for comparing the months. Table 1 summarizes the temperature and humidity records for the summer months. In both years there was an increase in the average temperature from May to August. The average relative humidity for each month in 1962 was higher than for the same month in 1961.

Table 2 shows the temperatures, rainfall, and snowfall at Athabasca, 40 miles east of Flatbush. The average temperatures are from one to four degrees lower at Athabasca than at Flatbush, but the general trend is the same in both places. However, rainfall is variable in the boreal forest. Snowfall was below average in 1960 - 61, and the following summer was warmer than average with normal rainfall, most of it in June and July. Snowfall was 36 inches above average in 1961 - 62 and the summer was cooler and with more rainfall than average (*in litt.* 1963 Meteorological Branch, Canada Department of Transport). Many of the habitats which were dry by June 1961 remained full of water in 1962. The level of Lake Sara, the largest lake in the area, remained ten to twelve inches higher in 1962 than in 1961.

TABLE 1

Temperature and Relative Humidity Records for 1961 and 1962

	May	June	July	August
	Temperature in degrees Fahrenheit			
1961				
Range:	28 - 83	44 - 92	42 - 87	44 - 86
Mean Maximum:	66.1	75.0	74.0	77.6
Mean Minimum:	41.7	51.3	51.4	51.1
Average:	53.9	63.1	62.7	64.3
1962				
Range:	20 - 76	38 - 88	41 - 85	40 - 86
Mean Maximum:	61.8	69.7	71.0	71.4
Mean Minimum	38.8	46.5	49.0	49.2
Average:	50.3	58.1	60.0	60.3
	Relative Humidity			
1961				
Range:	20 - 95	30 - 96	30 - 94	32 - 95
Mean Maximum:	87.4	89.2	89.7	90.0
Mean Minimum:	39.7	47.5	50.2	43.6
Average:	63.5	68.3	69.9	67.2
1962				
Range:	24 - 100	25 - 97	28 - 97	32 - 97
Mean Maximum:	94.8	93.5	94.7	94.8
Mean Minimum:	41.7	43.5	49.3	50.9
Average:	68.2	67.5	72.0	72.7

TABLE 2

Weather Data at Athabasca, 40 miles east of Flatbush, Alberta

Rainfall in Inches

	May	June	July	August	Total
1961	0.30	4.49	4.38	0.88	10.05
1962	2.32	3.99	4.88	2.49	13.68
Average - 30 years	1.75	2.52	2.87	2.33	9.47

Temperature in Degrees Fahrenheit

	May	June	July	August
1961	51.4	61.8	61.2	62.0
1962	48.0	56.7	59.7	56.4
Average - 30 years	48.6	55.8	60.4	57.5

Snowfall - Inches

Winter 1960 - 61	35.8
Winter 1961 - 62	93.9
Average - 21 years	58.0

Mean Date of first Frost:

Average - 29 years	19 August

1.3 Vegetation

Forests

Forests of aspen poplar, Populus tremuloides, dominate the countryside. Some of them are mature with typical associated vegetation, others are secondary forests with smaller, more closely spaced trees. The mature aspen forest rises 50 feet from the ground, and although the canopy is open, the shade may be dense in places (Fig. 3). Plants found in this habitat include:

Aspen poplar Populus tremuloides Michx.
Balsam poplar Populus balsamifera L.
White spruce Picea glauca (Moench)
Prickly rose Rosa acicularis Lindl.
Low-bush cranberry Viburnum edule (Michx.)
Red osier dogwood Cornus stolonifera Michx.
Involucrate honeysuckle Lonicera involucrata (Richards)
Bunch berry Cornus canadensis L.
Smooth wild strawberry Fragaria glauca (S. Wats.)
Tall lungwort Mertensia paniculata (Ait.)
Western Canada violet Viola rugulosa Greene
Dandelion Taraxacum officinale Weber
Common plantain Plantago major L.
Cream-coloured vetchling Lathyrus ochroleucus Hook.
American vetch Vicia americana Muhl.
Woodland horsetail Equisetum sylvaticum L.
Swamp horsetail Equisetum limosum L.
Twin flower Linnaea borealis L. var. americana (Forbes)

Fireweed *Epilobium angustifolium* L.

Wild sarsaparilla *Aralia nudicaulis* L.

The denseness of the shrub layer varies in the mature forest. Where cranberry and prickly rose form large dense stands, the herb layer is reduced to just twin flower. In the less dense areas, twin flower is associated with wild sarsaparilla. Many of the other herbs may be found along the forest paths or at the edge of the forest.

There are two types of immature aspen forest. The first, and younger type is closely spaced aspen poplar only 15 feet in height with little or no shrub layer (Fig. 4). The second and older type has a more open appearance, and dense shrub and herb layers (Fig. 5). Occasionally along the edges of paths, willow may be associated with the young aspen trees. The first type of immature forest contains:

Aspen poplar *Populus tremuloides* Michx.

Balsam poplar *Populus balsamifera* L.

Tall lungwort *Mertensia paniculata* (Ait.)

American vetch *Vicia americana* Muhl.

Two-leaved Solomon's seal *Maianthemum canadense* Desf.

Wild sarsaparilla *Aralia nudicaulis* L.

Smooth wild strawberry *Fragaria glauca* (S. Wats.)

The second, older type of aspen forest contains in addition:

Prickly rose *Rosa acicularis* Lindl.

Low-bush cranberry *Viburnum edule* (Michx.)

Red osier dogwood *Cornus stolonifera* Michx.

Beaked hazelnut *Corylus cornuta* Marsh.

Some pure stands of white spruce, *Picea glauca*, are found in the aspen forests. No shrub or herb layer grows under these trees; the lower branches are dead and the ground is covered with dead twigs. These trees provide important mosquito resting places.

The pin cherry, *Prunus pennsylvanica* L., and the choke cherry, *Prunus virginiana* L. var. *melanocarpa*, are found occasionally in glades in the forests. Extending out from the forests, willow trees form an open bushland (Fig. 6) where many small depressions in the ground fill up with water when the snow melts. Mosses and *Ledum groenlandicum* Oeder are associated with the willows.

Grasslands

Mixing with the willows are small patches of open grassland. Typical plants of these grasslands are:

Aspen poplar (young) *Populus tremuloides* Michx.

Balsam poplar *Populus balsamifera* L.

Canada blueberry *Vaccinium myrtilloides* Michx.

Wild red raspberry *Rubus strigiosus* Michx.

Prickly rose *Rosa acicularis* Lindl.

Few-flowered snowberry *Symphoricarpos albus* (L.)

Common blue-eyed grass *Sisyrinchium montanum* Greene

Dandelion *Taraxacum officiniale* Weber

American vetch *Vicia americana* Muhl.

Smooth wild strawberry *Fragaria glauca* (S. Wats.)

Northern bedstraw *Galium boreale* L.

Swamp horsetail *Equisetum limosum* L.

Vegetation near the Lake

The term 'muskeg' is frequently used for the swampy regions of northern Canada. However, Lewis, Dowding and Moss (1928) have defined muskeg as one of the stages in a vegetational succession. These stages are:

1. Aquatic stage
2. Low moor
3. Birch moor
4. Muskeg
   a) *Ledum* moor
   b) Young bog forest
   c) Mature bog forest
5. Climax forest

The first three stages contain water during the summer, and are suitable habitats for aquatic animals. The muskeg is a drier region of *Sphagnum* moss, *Ledum*, and trees. This distinction is also made by Dansereau and Segedas-Vianna (1952) who separate marshes and swamps, which rarely contain *Sphagnum*, from bogs which are dominated by this moss. It is the successional stages before muskeg is reached which are important for mosquitoes; the aquatic habitats to be described are included in the 'aquatic stage' and 'low moor' of Lewis, Dowding and Moss (*op. cit.*).

There are several lakes in the study area; the largest, Lake Sara (Fig. 7), has an area of three-quarters of a square

Fig. 3. The mature aspen forest. The path is bordered by grasses and willowherb. July, 1962.

Fig. 4. A semipermanent habitat (location 16) on a survey line in the immature aspen forest. May 1961.

Fig. 5. The older type of immature aspen forest with willow herb, wild sarsaparilla, twin flower and wild red raspberry covering the forest floor. July, 1962.

Fig. 6. Willow scrub near Lake Sara. <u>Aedes communis</u> breeds in the pools which form among the bushes. July, 1962.

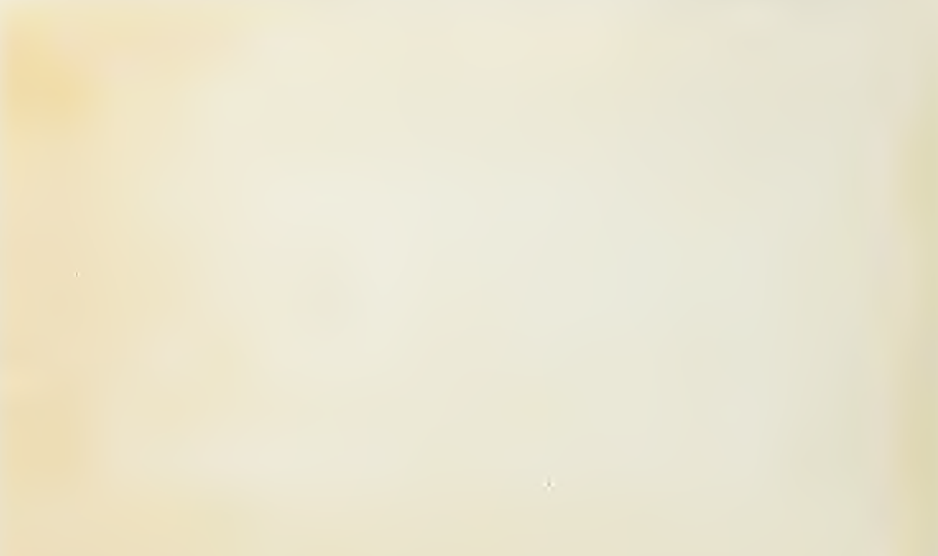

Fig. 7. Rearing cages at the edge of Lake Sara. The fringing vegetation is mainly sedge and horsetails. Some willows are growing in the shallow water. June, 1962.

Fig. 8. A permanent habitat at the edge of Lake Sara (location 2). The open water is seen at the right; most of the small willows in the foreground are dead. May, 1961.

mile. At the edge of the open water some aquatic plants may dominate a small area, for example the marsh marigold, *Caltha palustris*, or *Equisetum* spp. Further away from the open water there is a more compact type of vegetation often interspersed with willows, many of which have become waterlogged and died (Fig. 8). Water is permanently above this vegetation mat during the summer months.

Plants growing at the edge of the open water are:

Beaked sedge *Carex rostrata* Stokes

Rush *Juncus* spp.

Buck-bean *Menyanthes trifoliata* L.

Marsh marigold *Caltha palustris* L.

Arum-leaved arrowhead *Sagittaria cuneata* Sheld.

Tall cotton grass *Eriophorum angustifolium* Roth

Woodland horsetail *Equisetum sylvaticum* L.

Swamp horsetail *Equisetum limosum* L.

Greater bladderwort *Utricularia vulgaris* L. var. *americana* Gray

Moss *Drepanocladus revolvans* var. *intermedius*

Plants further back from the open water include:

Beaked sedge *Carex rostrata* Stokes

Rush *Juncus* spp.

Manna grass *Glyceria* sp.

Willow *Salix* spp.

Swamp birch *Betula pumila* L. var. *glandulifera*

Tall cotton grass *Eriophorum angustifolium* Roth

Marsh skullcap *Scutellaria epilobifolia* Hamilton

Buck-bean *Menyanthes trifoliata* L.

Smooth scouring rush *Equisetum laevigatum* A. Br.

Seaside arrow grass *Triglochin maritima* L.

Marsh cinquefoil *Potentilla palustris* (L.)

Greater bladderwort *Utricularia vulgaris* L. var. *americana* Gray

Moss *Drepanocladus vernicosus* (Lindb.)

Further still from the open water, the *Drepanocladus* spp. form small tussocks above the water. The beaked sedge and rush decrease in abundance as the willows increase. However, in lower ground among the willows, a *Drepanocladus* - *Carex* association is found (Fig. 9). The sedge forms 100 per cent of the herb layer casting a dense shade in the summer; the moss and matted remains of the dead sedge form a spongy substrate. These sedge marshes are important breeding places for mosquitoes before they dry up in the summer.

In one place on the east side of the lake, there is a more homogeneous *Carex* - *Salix* habitat where it is dry for most of the year, but in 1961 it was flooded after heavy rains. The plants found here are:

Beaked sedge *Carex rostrata* Stokes

Willow *Salix* spp.

Western dock *Rumex occidentalis* S. Wats.

Common nettle *Urtica gracilis* Ait.

Marsh hedge nettle *Stachys palustris* L. var. pilosa

Yellow avens *Geum aleppicum* Jacq.

Water persicaria *Polygonum natans* A. Eaton

A further stage in land colonization is the muskeg as defined by Lewis *et al*. (1928); water forms pools in the spring and by June the water is below the plant mat. This type of vegetation exists in only a few places in the study area and is not important. The trees associated with muskeg - white spruce, black spruce, and larch - are sometimes found on higher ground among aspen poplar, prickly rose, and beaked hazelnut. This sort of vegetation forms a dense shade.

Sloughs

Sloughs are common along the sides of the roads and in early spring they are full of water (Fig. 10). The shallow sloughs are covered with aquatic vegetation and will eventually dry up. Others have only marginal vegetation and an expanse of open water which will persist throughout the summer. The edges of the sloughs are thick with grasses and, in some places, shrubs. Characteristic plants are:

- Hairy wild rye *Elymus innovatus* Beal
- Northern reed grass *Calamagrostis inexpansa* A. Gray
- Timothy grass *Phleum pratense* L.
- Brome grass *Bromus inermis* Leyss.
- Common horsetail *Equisetum arvense* L.
- Swamp horsetail *Equisetum limosum* L.
- Wild red raspberry *Rubus strigosus* Michx.

while beaked sedge and swamp horsetail grow in the water.

Other aquatic habitats where mosquitoes breed are depressions in cart tracks and survey tracks passing through the

Fig. 9. A sedge marsh (location 3) near Lake Sara. Clumps of dead sedge break the water surface, and the marsh is surrounded by willows. May, 1962.

Fig. 10. A roadside slough (location 9). Sedges grow at the edge, but the centre of the slough remains open. This slough did not dry up. July, 1961.

Fig. 11. A grass habitat (location 10) in an exposed situation. Some willows are growing in the marsh; the nearest trees are 150 yards away. May, 1961.

Fig. 12. A forest habitat (location 5) with overhanging willow trees. June, 1961.

aspen forests (Fig. 4). These depressions sometimes merge with naturally occurring sedge or grass marshes. They dry up during the summer but may be refilled again by heavy rain, as in 1961. The moss, _Funaria hygrometrica_ Hedw., is common around the muddy edges of these habitats; other plants include:

Beaked sedge _Carex rostrata_ Stokes

Fireweed _Epilobium angustifolium_ L.

Northern grass of Parnassus _Parnassia montanensis_ Fern. and Rydb.

Grass Marshes

Grass marshes are found in open pastures (Fig. 11) and in low ground in immature aspen forests. One species of grass is usually dominant. These grasses grow quickly, and by early July they are four feet high. A moss, _Drepanocladus aduncus_ (Hedw.), forms a dense mat in some marshes, and where the water is deeper duckweed occurs. In one marsh, (Location 10), there are small clumps of willow. Typical plants in grass marshes are:

Marsh reed-grass _Calamagrostis canadensis_ (Michx.) (in open marshes)

Fowl manna-grass _Glyceria striata_ (Lam.) (in aspen forest marshes)

Marsh cinquefoil _Potentialla palustris_ (L.)

Marsh skullcap _Scutellaria epilobifolia_ Hamilton

Marsh horsetail _Equisetum palustre_ L.

Moss <u>Drepanocladus aduncus</u> (Hedw.)

Moss <u>Drepanocladus revolvans</u> var. <u>intermedius</u> (Lindb.)

<u>Other Vegetation</u>

There are hedgerows of prickly rose and wild red raspberry between some of the cultivated fields. These broad leaved shrubs produce a more humid, cooler atmosphere than in the open, and sometimes mosquitoes are found resting in this vegetation during the day.

The Pembina and Athabasca rivers run through deep valleys some 200 feet below the general level of the country. Both rivers are turbid and fast flowing during the summer months. The slopes of the valleys are forested with aspen and associated shrubs. Parts of the east slope of the Athabasca valley are sandy and covered by white spruce. An oxbow lake has recently been isolated from the Pembina River.

Floras by Budd (1952) and Moss (1959) were used to identify the plants. A fuller description of the aspen parkland has been given by Bird (1961), and the vegetational zones of Alberta have been described by Moss (1955).

2. MOSQUITO SPECIES

2.1 Mosquito Species

Twenty five species of mosquitoes have been recorded in the study area in 1961 and 1962 (Table 3). The genus *Aedes* is the most important, and practically all the adult mosquitoes in June, July and August belong to this genus. The four remaining genera are not common except for two species, *Anopheles earlei* and *Culiseta alaskaensis*, which may be found indoors in May before the *Aedes* species have emerged. Mosquitoes were also collected in study area during the summer of 1960 (Pucat, 1960). The nomenclature is taken from Carpenter and LaCasse (1955). Keys to the larvae and adult females of the 5 genera and 25 species are given in Appendix 1.

2.2 Life Histories of Mosquitoes

Mosquitoes show five types of life history. Bates (1949) described four; the fifth has only recently been recognised (Frohne, 1954a) and is only found in arctic and subarctic mosquitoes.

1. *Aedes cinereus* type: there is only one generation per year; overwintering is in the egg stage, and the adults emerge in the spring. This is the most important life history in arctic, subarctic, and temperate regions.

2. *Aedes caspius* type: is similar to 1. but there may be more than one generation each year. This life history is more typical of tropical mosquitoes.

TABLE 3

Mosquito Species recorded at Flatbush, Alberta, 1961 and 1962, and their abundance.

A = Abundant; C = Common; O = Occasional; R = Rare

* Found only as an adult

** Found only as larvae

Genus AEDES Meigen	
Subgenus *Aedes* Meigen	
Aedes cinereus Meigen	C
Subgenus *Aedimorphus* Theobald	
Aedes vexans (Meigen)	A
Subgenus *Ochlerotatus* Lynch Arribálzaga	
Aedes canadensis (Theobald)	R *
Aedes cataphylla Dyar	R
Aedes communis (de Geer)	C
Aedes diantaeus Howard, Dyar, and Knab	R
Aedes excrucians (Walker)	C
Aedes fitchii (Felt and Young)	C
Aedes flavescens (Müller)	O
Aedes implicatus Vockeroth	O
Aedes intrudens Dyar	C
Aedes pionips Dyar	R
Aedes punctor (Kirby)	A
Aedes riparius Dyar and Knab	C
Aedes spencerii (Theobald)	O
Aedes sticticus (Meigen)	R

TABLE 3 (continued)

Genus AEDES Meigen	
Subgenus *Ochlerotatus* (continued)	
Aedes trichurus (Dyar)	R
Genus ANOPHELES Meigen	
Subgenus *Anopheles* Meigen	
Anopheles earlei Vargas	C
Genus CULEX Linnaeus	
Subgenus *Neoculex* Dyar	
Culex territans (Walker)	O
Genus CULISETA Felt	
Subgenus *Culicella* Felt	
Culiseta morsitans (Theobald)	R **
Subgenus *Culiseta* Felt	
Culiseta alaskaensis (Ludlow)	O
Culiseta impatiens (Walker)	R
Culiseta incidens (Thomson)	R
Culiseta inornata (Williston)	R *
Genus MANSONIA Blanchard	
Subgenus *Coquillettidia* Dyar	
Mansonia perturbans (Walker)	R *

3. *Anopheles claviger* type: overwintering is in the larval stage and the adults emerge in late spring or summer; there is one generation each year. This life history is shown by mosquitoes in England (Marshall, 1938), Denmark (Wesenberg-Lund, 1921), and probably in the study area, *e.g.* by *Mansonia perturbans*.

4. *Culex pipiens* type: there are many generations each year, and overwintering (hibernation) is in the inseminated female stage. This is a common life history in the tropics.

5. *Culiseta impatiens* type: of the genus *Culiseta*, and *Anopheles earlei* and *Culex territans* in temperate regions. The inseminated adult females hibernate during the long winter and eggs are laid in the spring. There is one generation per year and adults emerge in July and August.

Life histories 1. and 5. are the most important ones in the study area. The seventeen *Aedes* species follow the *Aedes cinereus* type; the *Culiseta*, *Anopheles*, and *Culex* species follow the *Culiseta impatiens* type; while *Mansonia perturbans* presumably follows the *Anopheles claviger* type although this has not been confirmed.

These differences in life history result in adults occurring at different times of the year. Fig. 13 shows the life histories of the principal species in the study area. *Aedes canadensis*, *A. diantaeus*, *A. trichurus*, and *Mansonia perturbans* were too rare to permit accurate analysis of their life histories. The *Culiseta* species, other than *Culiseta*

alaskaensis, are also rare, but their life histories are sufficiently similar (Frohne, 1954b) to be included with this species.

Most of the species show the *Aedes cinereus* type of life history and it is the synchronization of emergence that causes the sudden appearance of mosquitoes in late May (Figs. 18 and 19). Even within the genus *Aedes* there are differences. *A. communis*, *A. implicatus*, *A. punctor*, *A. riparius*, and *A. spencerii*, are the first to hatch in the spring (Fig. 13). *A. excrucians*, *A. fitchii*, *A. pionips*, and *A. vexans* hatch later while *A. cinereus* and *A. sticticus* do not hatch until mid May. The fluctuations in the adult population are discussed in section 5.1. Some species, *e.g.* *A. implicatus* and *A. flavescens* were only found during a short period of time, but this does not necessarily mean that they were short-lived. For instance, adults of *A. spencerii* were found on 30 May 1962 and one female on 9 September; none were seen in between these dates and since larvae were not found after May, it is assumed that the September specimen was a remnant of the spring population. In 1961, a dry hot year, *A. fitchii*, *A. riparius*, and *A. intrudens* were not found after the end of June - a marked contrast to 1962.

In both years, there was a gap of two to three weeks between the emergence of *A. vexans* and their appearance in the flight activity samples. In 1961, *A. vexans* and *A. excrucians* larvae were found early in July after heavy rains. These

larvae were a second brood hatched from eggs which had remained dormant from the previous year.

Adults of species with the *Culiseta impatiens* life history are found in March, April, and May. In the spring they bite readily and enter buildings (Section 5.7). Eggs are laid and larvae develop after all the *Aedes* species have emerged. Adults of the new generation which emerge late in the summer are seldom seen. Three swarms of *Anopheles earlei* were observed in September 1962 (Section 5.8). Few female *Anopheles* of the new generation were seen in the late summer of 1961 or 1962.

Since the life histories of *Anopheles earlei* were different in 1961 and 1962, both are included in Fig. 13. Adult *Anopheles* disappeared by the end of May, and larvae were found from mid May to the end of July in 1961. In 1962 adults persisted until the end of July and frequently bit indoors. Larvae did not appear until the end of July. Similar differences were seen in *Culex territans* and the *Culiseta* species. In 1961, the early mortality of these species, *Anopheles earlei* in particular, may have been due to the hot dry weather. Consequently eggs were laid and hatched early in the season. More favourable weather in 1962 allowed much of the population to remain until late July. In neither year did larvae appear until just before the last adults were seen.

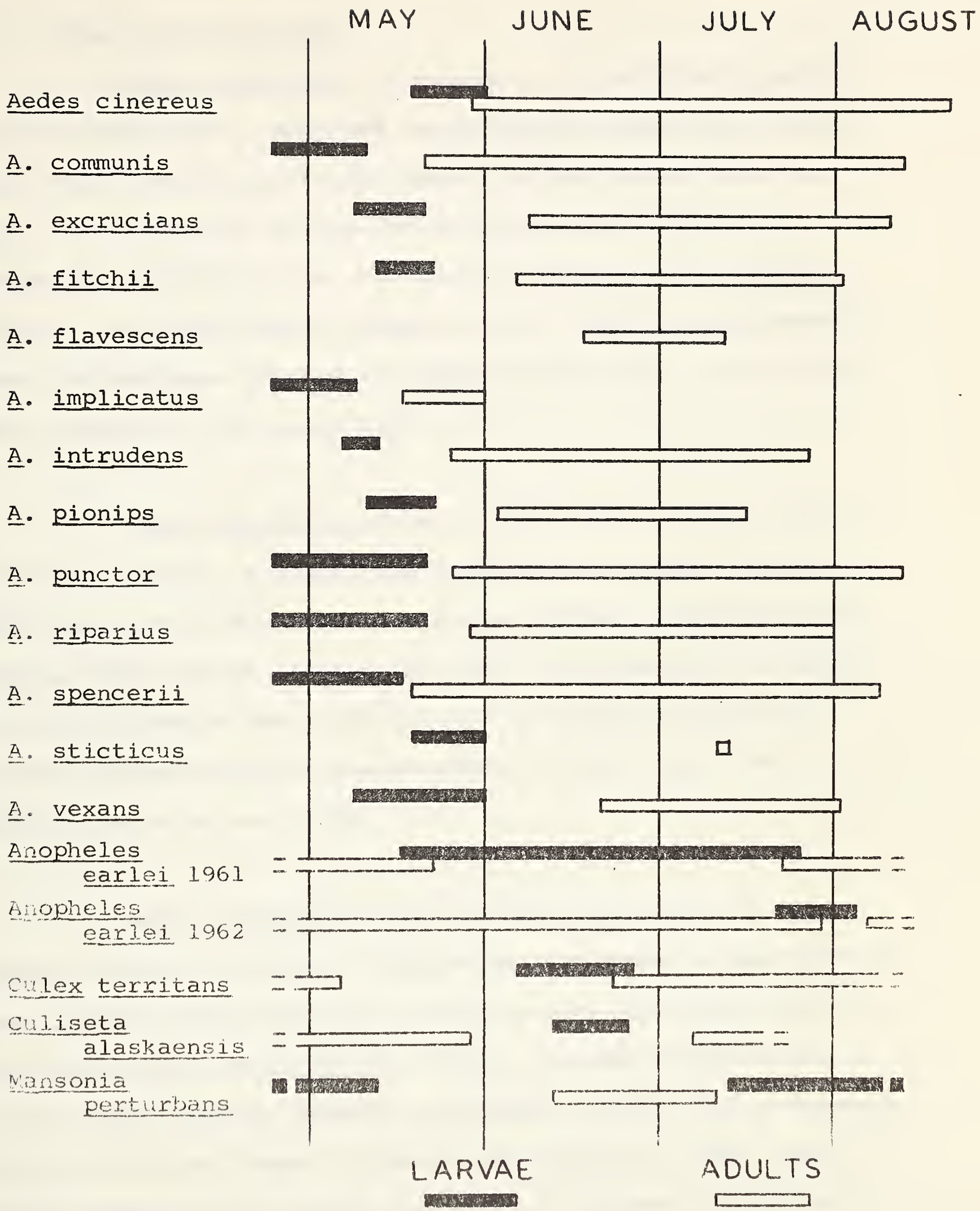

Fig. 13. Life Histories of some mosquitoes at Flatbush, Alberta based on the 1961 results except where indicated. Emergence was up to a week earlier in 1962.

2.3 Notes on the species

Aedes canadensis (Theobald) is a very rare species in the study area. Only two adult females were caught; one on 4 July 1962 biting in the forest at 0030 hours (Section 5.5), and the other during the afternoon of 7 July 1962. Shemanchuk (1959) did not record this species from southern Alberta; in Saskatchewan (Rempel, 1950, 1953) it is commonest near the northern edge of the aspen grove region, an environment similar to the study area.

Aedes cataphylla Dyar, in some years a major pest at Edmonton, 100 miles south, was rare in both years. Larvae were found on 23 May 1961 in a grass habitat, and three adult females were caught in late May 1962. This species is found in most of Saskatchewan (Rempel, 1953) where it breeds in grassy depressions; the larvae appear in late April and adults emerge by early May.

Aedes cinereus Meigen is one of the last of the *Aedes* species to emerge. The larvae were found in mid to late May in open grass habitats. Other authors have found them in open and wooded pools (Haufe, 1952), in pools under alder, willow, and dogwood (Jenkins and Knight, 1952), and in ditches at the border of lakes in Scandinavia (Natvig, 1948). The adults emerge at the end of May ......"they were first seen on 28 and 30 May 1962 flying among the emergent grasses of their breeding place, and resting on the dead vegetation or

on the water surface. They never tried to land on me, or bite me" (field notes). Later in the summer, adult *A. cinereus* remain in the forests and in shaded valleys, not at their breeding habitats. Although adults emerged by 30 May 1962, none were caught in the evening samples (Section 5.1) until 10 June.

Wesenberg-Lund (1921) remarks that this species stays close to the ground (which is true for the first days of its adult life) and that it has difficulty in biting. It was an annoying biter in the forests.

Aedes communis (De Geer) is a well studied species because of its abundance in some areas (Wesenberg-Lund, 1921; Natvig, 1948; Haufe, 1952, 1957; Frohne, 1956). All authors agree that it is a woodland species. The larvae were found in clear pools shaded by willows, and less commonly in well shaded sedge habitats. The adults emerge by the end of May. In cold pools emergence may be delayed until late June (*e.g.* Cage V, Section 3.4).

This species is a particularly annoying biter in the willow scrub (Section 5.6). Curtis (1953) found it outnumbered all other species in collections taken on man in Yukon Territory. In June and July 7—8 per cent of the mosquito population in the aspen forest was this species. Adult *A. communis* may be found in mid August.

Aedes diantaeus Howard, Dyar and Knab is a rare

species. A few larvae were found in a forest pool in 1961, and several were found in sedge and semipermanent habitats in 1962. Three adult females emerged into a rearing cage during the transplant experiments. According to Carpenter and La-Casse (1955) most authors consider A. diantaeus a woodland species. Shemanchuk (1959) did not find it in southern Alberta, and it is rare in Saskatchewan (Rempel, 1953).

Aedes excrucians (Walker). This large is common in the study area particularly at the beginning of the summer. Larvae were found in shaded regions of sedge, grass, and forest pools. Wesenberg-Lund (1921) and Rempel (1953) also recorded it in shaded areas, but Natvig (1948) found it in open areas in Scandinavia. In Alaska (Gjullin et al., 1961), this species breeds in semipermanent pools when there is an emergent cover of Carex rostrata or Equisetum fluviatile L. In 1962 there was only one brood; in 1961 a second brood hatched early in July after the heavy rains.

The females are active biters in forest and in the open. Early in the summer this species, A. riparius, and A. fitchii are the main species in the open. Natvig (1948) records that adults are active when the temperature is high and the sun is shining. The population curve is shown in Figs. 18 and 19; however, adults are still flying in open habitats after they have disappeared from the forest. In June and July 7-10 per cent of the mosquitoes in the aspen forest were this species.

Aedes fitchii (Felt and Young). Like the previous species, this is found in the open and in the willow scrub early in the season. Although not numerous, 24-hour counts show that is flies at any hour and will bite at night. The females are common in June, but numbers decline in July and August. In June and July 1961, 5% of the population in the aspen forest was this species; in 1962 the corresponding figure was 11%. The larvae were found in grass and semipermanent habitats. It made up 10 per cent of the population at Goose Bay (Haufe, 1952), and Curtis (1953) found it was active mainly during the hours of darkness and in the early morning. Dr. J. R. Vockeroth (Entomology Research Institute, Ottawa, *in litt.*, 1961) thinks that females of this species cannot be distinguished from females of *A. stimulans* (Walker); in this study possible *A. stimulans* were identified as *A. fitchii*.

Aedes flavescens (Müller) is a rare species here although it is common on the prairies of Saskatchewan (Rempel, 1953) and Alberta (Shemanchuk, 1959). Hearle (1929) considered it the second most abundant species on the prairies.

The larvae were found in semipermanent habitats. Adult females were caught in a lucerne field when the sun was shining and the temperature was 66° F; males and females were flying over wet grass at 0530 hours when the sun was rising and the air was nearly saturated. Hearle (1929) remarks that they fly throughout the day and are especially active at dusk. Very large yellow mosquitoes, probably *A. flavescens*, were

flying in the canopy layer of the forest soon after dawn on 20 June 1962.

Aedes implicatus Vockeroth is an early species. Larvae have been found in sedge, grass, semipermanent, and forest habitats. In 1962, two adult females were caught on 17 May, the first *Aedes* flying. It is not a common species; nine specimens were caught in the forest samples in June and July 1961, and seventeen in 1962. None were seen after mid June in 1962. Nielsen and Rees (1961) also found that this species is short lived and adults rarely survive after mid July.

Aedes intrudens Dyar is an important species because it enters buildings (Dyar, 1928; Carpenter and LaCasse, 1953; Nielsen and Rees, 1961). The larvae were found in grass and semipermanent habitats and the adults emerged by the end of May. Although it is a forest species (Carpenter and LaCasse, 1955), most specimens in the study area were caught inside buildings. A few were captured in the woods until the end of June; thereafter all specimens were found indoors where they were very annoying. This species made up nearly 50 per cent of all the mosquitoes caught in the hut during 1962 (Section 5.7). However, Matheson (1944) has never found this species in houses. At Waskesiu, Saskatchewan (Rempel, 1953), *A. intrudens* formed about 50 per cent of the mosquito population in the last two weeks of July, 1930.

Aedes pionips Dyar is one of the later developing species. The larvae have only been found in forest habitats where the water is clear, the substrate is covered with dark dead leaves, and where there is no emergent vegetation. It is a rare species; few adults were caught in the field but some were reared from larvae.

Aedes punctor (Kirby). This species and *A. vexans* were the most numerous in the study area. As might be expected of a widespread species, it is not selective in its breeding habitat. Larvae were found abundantly in sedge habitats, but also in grass, semipermanent, and forest habitats. Other authors (Haufe, 1952; Jenkins and Knight, 1952; Natvig, 1948) have also recorded a variety of breeding habitats.

The adults emerge by the end of May. They formed a very important part of the total mosquito population, 33 per cent in June and July in the aspen forest. They are numerous in willow scrub and common in the open, but they are seldom found at the sedge marshes during the day. The population curve of this species is shown in Figs. 18 and 19; in 1961 it contributed to three of the population peaks and in 1962, to all five population peaks. It is a persistent biter during the daytime and it also bites at night. Curtis (1953) found that it was the most active of the nocturnal mosquitoes at Whitehorse in the Yukon. There is no evidence that *A. punctor* enters buildings in the study area, although it is "often found in houses, cow stables and hog pens" in mountainous regions of

Scandinavia (Natvig, 1948).

Aedes riparius Dyar and Knab is similar in many ways to *A. fitchii*. The larvae are found in grass, sedge, and semi-permanent habitats in late April and May. The adults emerged at the end of May; they are common in June, but only a few remain in July and August. This species is tolerant of high temperatures and sunshine; it was found flying and biting early in the summer in the open when the only other species flying were *A. excrucians* and *A. fitchii*. More specimens were found outside the forests than inside; they were particularly common in willow scrub and near sheltered patches of open water. The curves of the population are shown in Figs. 18 and 19; in the aspen forest this species formed 8 - 10 per cent of the total mosquito population.

Aedes spencerii (Theobald) is primarily a prairie species and is rare in the study area. At first it was thought to be common because the second and third instar larvae of the abundant *A. punctor* were confused with those of *A. spencerii*. The larvae were found in open grass habitats and the adults were also found in open situations. Only one adult female was seen in 1961 (9 May) while in 1962 two separate groups of adults attacked me on sunny afternoons in late May. One female was caught on 9 September 1962.

The bite from this species is particularly painful and lingering.

Aedes sticticus (Meigen) is another rare species. Larvae have been found mainly in semipermanent pools, but also in sedge and forest habitats. Adults were captured on 18 - 23 July 1961 in the forest samples, and near one of the forest locations (15) on 31 July 1961. They were found near this same location in June 1962 and were very eager to bite. In 1961, a second brood of *A. sticticus* larvae hatched in mid July.

Aedes vexans (Meigen) was one of the most abundant species and one of the most annoying. The larvae were found in grass and semipermanent habitats, and less frequently in sedge marshes, during the last half of May. They are one of the last of the *Aedes* species to emerge. Although there were no larvae after May, adult females were not found in the forest samples until mid June, *i.e.* there is a longer gap between pupation of the larvae and the appearance of the adults than in other species. *A. vexans* is known to be multivoltine (Wesenberg-Lund, 1921; Gjullin *et al.*, 1950; Rempel, 1953; Nielsen and Rees, 1961) if climatic conditions are suitable. In 1961, a second brood of larvae developed in early July, so that subsequently the adult population was higher than at any previous time during the season (15 - 25 July; Fig. 18). Reflooding of the habitats which had already dried up caused this appearance of the late brood. The *Carex-Salix* habitat on the east side of Lake Sara was an important breeding ground. The *A. vexans* population never reached the level in 1962 that it did in 1961.

This species can fly under many climatic conditions. It is active in the open when the sun is shining. On 2 August 1961 females were flying in the open when the temperature was 82°F and the relative humidity was 45 per cent. It bites during the hours of darkness. Its numbers, wide range of flight conditions, and biting habits, make it one of the most annoying species. In June and July 1961 24 per cent of the woodland population were _A. vexans_, but only 16 per cent in 1962. The 1961 percentage was increased by the second brood in mid July.

A. vexans shows much variation in the pattern of the black and white scales of the abdominal tergites but whether this has any significance is not known.

Anopheles earlei Vargas was the second most numerous species found in buildings, especially in April and May. These adult females, which had overwintered from the previous autumn, bit readily. The differences in the 1961 and 1962 life histories are summarized in Fig. 13. Larvae were found in open permanent habitats and the adults emerge in July or August but are rarely seen until the following spring. A female was seen on 11 August 1961 and two swarms of males were observed on 14 September 1962. No males have been seen in April or May so it is presumed that, as in the _Culiseta_ species, only the inseminated females hibernate. Pratt (1953) observed that this species will bite man in bright sunlight, but in the study area very few were found outside buildings.

Culex territans (Walker). This species also hibernates as an adult. The larvae have been found in sedge and grass habitats and occasionally in semipermanent and permanent habitats. They are not found until mid June (after all the *Aedes* species have emerged); in 1961 larvae could be found until August but in 1962 none were found after the end of June.

Adults are rarely seen since they feed on amphibians and are not attracted to man (Carpenter and LaCasse, 1955). No adults were seen in 1961 but some females were observed on 27 April 1962: "It had rained overnight but now the sun was shining and occasionally there was a light breeze. As soon as I arrived at the slough some mosquitoes (later identified as *C. territans*) flew up from the decayed sedge by the water. Other mosquitoes were flying three to six inches above the open water surface. Sometimes one would alight on the water surface for a few seconds, and then take off again. Then it would fly back to the decayed vegetation and be lost to view since its colour was similar to that of the dead leaves and stems..........By about 4 p.m. the sun had gone in and no mosquitoes were flying; they were difficult to find amongst the vegetation. Not one landed on me or seemed interested in me during the hour I was watching them" (field notes). Adults, reared from larvae in 1962, emerged from 19 June to 5 July.

Culiseta alaskaensis (Ludlow). Females of this large

species overwinter (Frohne, 1954b) and are flying by mid April. Only two females were caught in 1961, but in 1962 they were numerous in buildings in April and May when they were attracted to humans and domestic animals. No larvae were found in 1961, and only a few in a grass habitat in 1962. Natvig (1948) considers this an 'archiboreal' species and suggests that is probably survived the Ice Age both north and south of the region of maximum glaciation. It is common in Alaska (Gjullin et al., 1961) but rare in Alberta and Saskatchewan.

Culiseta impatiens (Walker) is a very rare species. Twelve larvae were found in a grass habitat (10) on 18 July 1961. No adults have been found. Frohne (1953) has made an extensive study of this species in Alaska.

Culiseta incidens (Thomson) is also a rare species. A few larvae were found in grass and sedge habitats in early August 1961, and three more were found in a grass marsh in June 1962. A badly damaged female captured in the hut on 13 July 1962 may be this species.

Culiseta inornata (Williston) is another rare species in the study area. A group of adult females was flying in a rainstorm in a small valley of willow trees (Location 5) on 30 June 1961. In 1962, two females were caught in the forest samples at the end of July; two others were attracted to a kerosene pressure light in mid July. This species is common

on the prairies (Rempel, 1953; Shemanchuk, 1959) but rare in the aspen forest at Flatbush. No larvae were found.

<u>Culiseta morsitans</u> (Theobald). This species is also rare. Four larvae were found in a grass habitat on 30 May 1961 and a few larvae were present in grass and sedge marshes from 7 May to 24 June 1962. Jenkins (1948) also found larvae in sedge sloughs in Alaska.

No adults were seen.

<u>Mansonia perturbans</u> (Walker). One female of this species was caught in the hut on 27 June 1961, but no more were seen until July 1962. Adult females were attracted at night to a kerosene pressure lamp 50 yards from Lake Sara (Fig. 2). Others were captured indoors, presumably after being attracted by the light, and in the forest at ground, 20 feet, and 40 feet levels during the night. Burgess and Haufe (1960) also found this species above the forest floor, at 25 and 50 feet, in an elm wood in Ontario, and Snow and Pickard (1957) caught it at 30 and 50 feet in a cypress forest in Tennessee. This species is a persistent biter and would be a serious pest if it were more numerous. Edwards (1932) has described the life history of <u>Mansonia perturbans</u>; if it follows the same life history in northern latitudes, it will be the only species to overwinter as a larva. Attempts to find the larvae were unsuccessful despite the variety of methods tried and the types of plants examined (<u>Sagittaria</u>,

Typha, *Nuphar*, *Equisetum*).

This species has been reported from British Columbia and Saskatchewan (Carpenter and LaCasse, 1955), but not previously from Alberta.

3. HABITATS OF LARVAE

3.1 Classification of Habitats

There are many classifications of natural waters but none of them are entirely satisfactory when considering mosquito breeding in temperate latitudes. Some are based on the origin of the water, others on the location and condition of the water. Bates (1949) divided natural waters into four groups: 1) Permanent or Semipermanent, 2) Running water, 3) Transient ground pools, and 4) Container habitats. Laird (1956) considers this classification does not allow a comparison of the adaptations of mosquitoes to specialized environments, so he proposed another classification based on freshwater and brackish water, each with subdivisions into surface water and container habitats.

For present purposes Bates' classification is better although some changes are necessary. Only the first of Bates' groups is important in the study area. On the basis of position, permanence, and the amount of shading by plants, the larval habitats were divided into five types:

Sedge marsh, water temporary I

Grass marsh, water temporary II

Open habitat, water permanent III

Open habitat, water semipermanent IV

Forest habitat, water temporary, overhung by trees..V

Sedge Marsh (I)

The sedge, *Carex rostrata*, marshes are the most numerous of all mosquito breeding habitats in the study area (Fig. 9). They are found along the margins of Lake Sara, well back from the deep water, and in sloughs which extend outwards from the lakes among clumps of willows (Section 1.3). The water level in the sedge marsh is regulated by the water level of the lake. In 1961, the marshes had dried up by mid June; in 1962 they did not dry up at all. In the spring, they have no emergent vegetation except for clumps of dead, dry sedge which are surrounded by snow melt water containing *Aedes* larvae. By late May the new growth of the sedges is 12 inches high, the surrounding willows are in leaf, and most of the mosquitoes have emerged. By the end of June, the sedges are three feet high casting a dense shade over the marsh. In August the vegetation may be four feet high and beginning to turn yellow, and by September most of the sedge has died. The substrate is covered by a moss, *Drepanocladus*, which forms a spongy mass isolating the remaining pools of water as the water level falls. The sedge habitats are characterized by almost 100 per cent *Carex rostrata*, with an occasional horsetail or marsh marigold, and they are protected from wind by the surrounding trees.

Grass marsh (II)

Grass marshes contrast with sedge marshes since they are found in exposed situations, and are rarely surrounded by

trees (Fig. 11). The grass is either marsh reed grass, Calamagrostis canadensis, or fowl manna grass, Glyceria striata if the habitat is sheltered. Since these plants do not grow in water more than two or three feet deep, grass marshes often have open water in the centre. Like the sedge marsh, they are covered with tussocks of dead vegetation in May, but new growth rapidly shades the water and by July the grass may be over four feet high. In most places the grass falls over so that little of the water surface is visible. The substrate is covered by spongy Drepanocladus moss. Parts of the marsh remain covered with water all through the summer but the marginal areas usually dry up by mid June.

Open habitat, water permanent (III)

There were only two lakes of permanent water in the study area. One was Lake Sara, threequarters of a square mile in area (Fig. 7); the other was the oxbow lake isolated from the Pembina river. The emergent vegetation along the edges of the lakes was frequently blown and disturbed by strong winds. The vegetation was varied but scanty (Section 1.3) providing little shade. Ducks, grebes, common loons, and black terns nested among this vegetation. Drepanocladus moss formed a very dense spongy substrate below the water surface. Because of the size of the lakes, the water level did not vary more than two or three inches during the summer of 1961. Further back from Lake Sara were sedge marshes and willows (see earlier), but the steep sides of the river gorge

prevent this formation at the oxbow lake. Included in this habitat type are the larger roadside sloughs with deep water (Fig. 10). The sides were fringed with sedge, but the deeper water remained open with patches of duckweed, _Lemna minor_ L., floating among the sedge and at the lee end of the slough.

Open habitat, water semipermanent (IV)

The semipermanent waters show characteristics of all the previous types. They are small roadside sloughs and water filled depressions in cart tracks and survey tracks (Fig. 4). The vegetation, normally sedge, may be dense in places around the edge, but the centre contains open water less than 12 to 18 inches deep so that it dries up by midsummer. Mosses, for example _Funaria hygrometrica_, grow along the muddy edges. There is little shade except along the margins of the habitat, and even there, the vegetation may be flattened by wind.

Forest habitat (V)

The forest habitats have no vegetation growing in the water (Fig. 12). Shade is provided by the trees and shrubs whose branches form a canopy over the water. Leaves in all stages of decay form the substrate and the water is clear. In a normal year these pools dry up by mid or late June, but in 1962 water remained until September. Most of the pools in this group were found in willow scrub where Labrador tea, _Ledum groenlandicum_ Oeder, and _Drepanocladus_ moss were growing; none

was found in the aspen forests. In one place, immature aspen forest was inundated by lake water, forming a habitat similar to those in the willow scrub. *A. communis* larvae were abundant, as in the forest pools.

Aedes larvae and pupae develop before the main growth of the aquatic plants and before the appearance of leaves on the surrounding trees. *Culex*, *Culiseta*, and *Anopheles* larvae are found in July and August in those habitats which contain water throughout the summer so that these larvae develop under different conditions to *Aedes* larvae (Section 3.2). In the habitats with patches of open water, larvae are found mainly along the edges among the vegetation where wind action is least. Although the variation in habitats is limited, this is compensated for by their size and number.

Sixteen locations (numbered 1 to 16) were chosen in 1961 for detailed observation throughout the summer. They were chosen to represent the five habitat types and as wide a variation as possible. At the beginning they were not classified into the types described, but after study, they were found to fit as follows:

Habitat Type	I	II	III	IV	V
Location	3	4	2	6	1
numbers	8	10	9	7	5
	12	13	14	15	11
	17			16	

The five habitat types are not always clear-cut

and some of the locations could be placed in either of two habitat types; e.g. location 15 could be placed in types IV or V. In 1962, location 17, a sedge marsh was added to the list, and for various reasons locations 2, 9, and 14 were not visited.

3.2 Physicochemical conditions of Habitats

In 1961, measurements of pH, oxygen concentration, and temperatures at one inch and six inches below the surface were taken during each visit to a location until the water level became too low. Only temperature measurements were taken in 1962. None of these appear to have any limiting effect on mosquito populations.

In many pools the six inch temperature was taken in the moss mat, particularly later in the summer. The pH was recorded with pH papers, the water for measuring oxygen concentration was collected in a modified Klemmerer tube and the oxygen was determined by the Micro-Winkler method. The results of these observations are shown in Fig. 14.

All temperatures in late April were just above freezing point. However, before the aquatic and fringing vegetation had begun to grow, the surface temperatures rose to 70° to 80°F in the daytime. In most habitats the temperature dropped slightly during the summer, despite the increasing mean air temperature, since the vegetation formed more shade. The six inch temperature is probably a more reliable indication

of temperature differences between habitats since there is less daily fluctuation.

In most locations the one and six inch temperatures follow a parallel course. In sedge and grass dominated habitats where a moss mat is present, the six inch temperature is much lower than the one inch temperature; it remains lower throughout the summer although by August there is only a difference of two or three degrees. For instance, at location 3 on 22 May 1961, the one and six inch temperatures were 81° and 56°F respectively. The most productive habitats show this pattern. This insulating effect of the moss mat results in a steep temperature gradient through which the larvae have to move.

The temperature patterns of the habitats in 1962 were similar. However, by early May the six inch temperature was up to ten degrees higher than at the same time in 1961; by midsummer, the readings were almost the same as in 1961 and any differences were probably due to the larger water volume in 1962. The snow melted earlier in 1962 so that the water warmed up sooner even though the air temperatures were lower (Section 1.2). There was twelve inches of wet snow on 4 May 1962 but this did not have a long lasting effect on the rise in water temperature. The earlier warmth in May probably explains why the adult mosquito population emerged several days earlier in 1962 than in 1961.

Oxygen concentrations are expressed as cubic centimetres of free oxygen per litre of water. (Alternatively the

Fig. 14. Pages 50, 51, 52, 53, and 54.

Temperature and oxygen concentration of the water of the habitats in 1961. The number of each location is indicated at the top right corner of each graph. Data for locations 1. and 7. are not included.

△— — △ oxygen concentration;

○———○ temperature at one inch;

●———● temperature at six inches;

D - dried up.

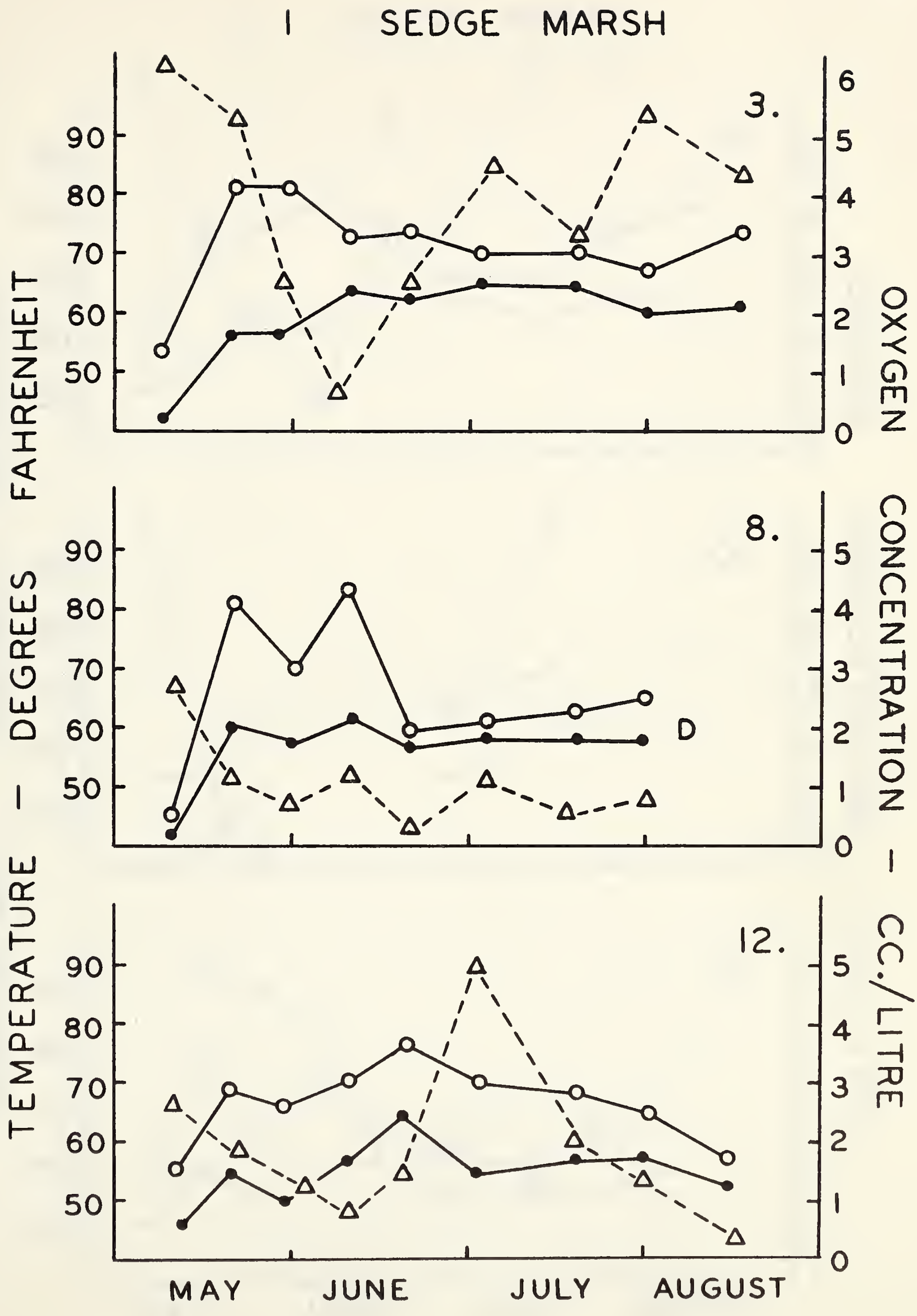
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Fig. 14

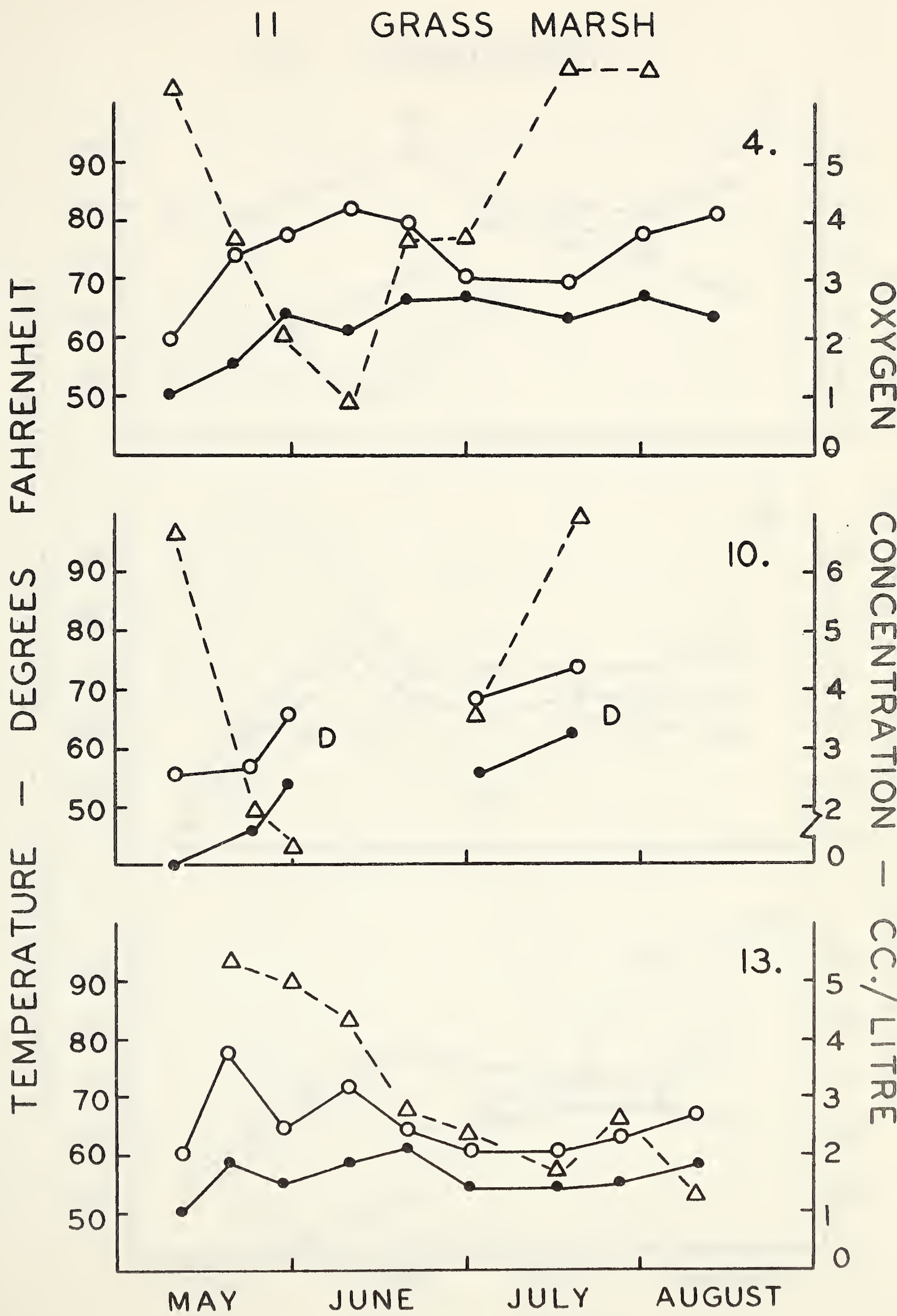
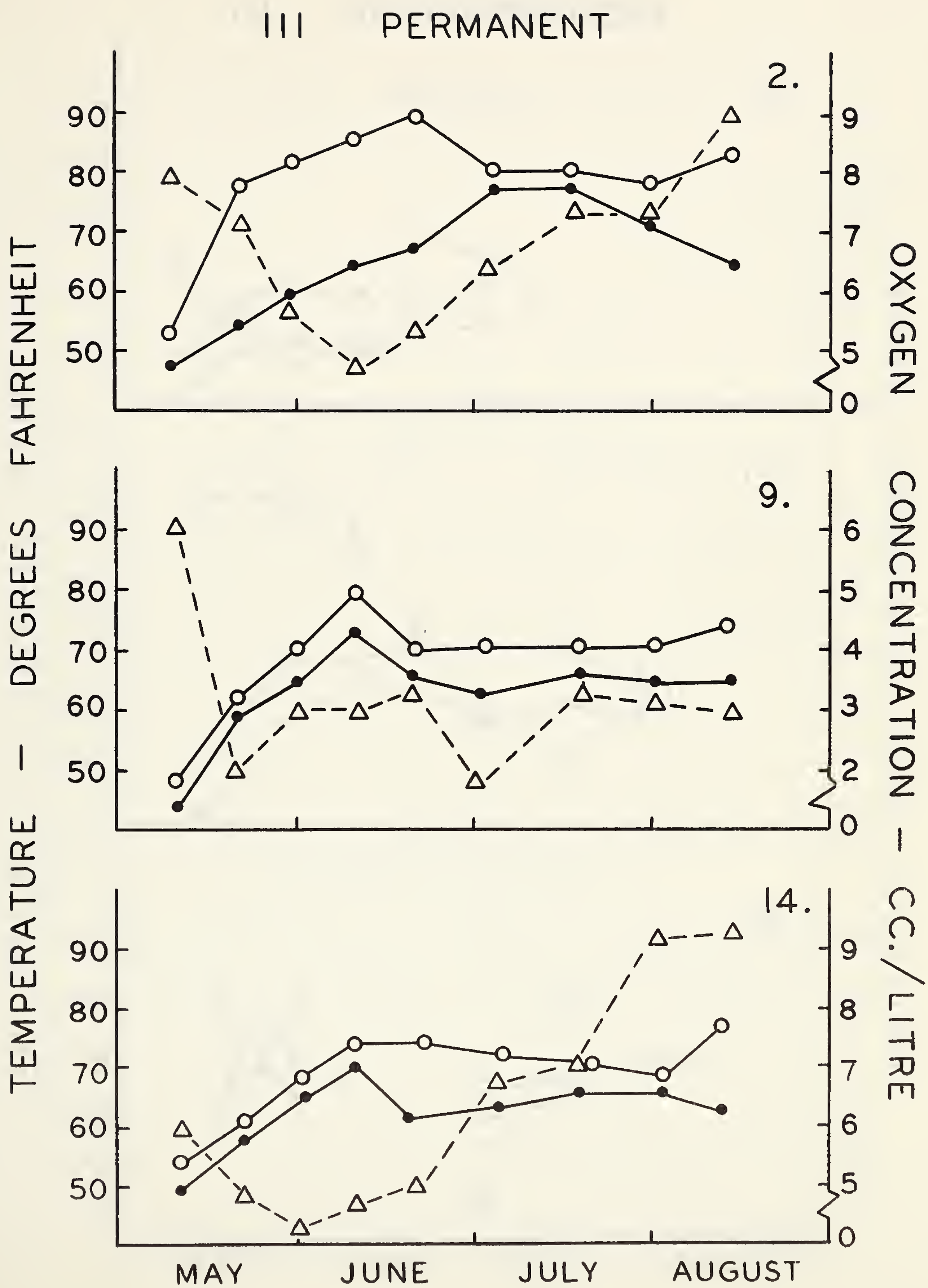


Fig. 14 (continued)



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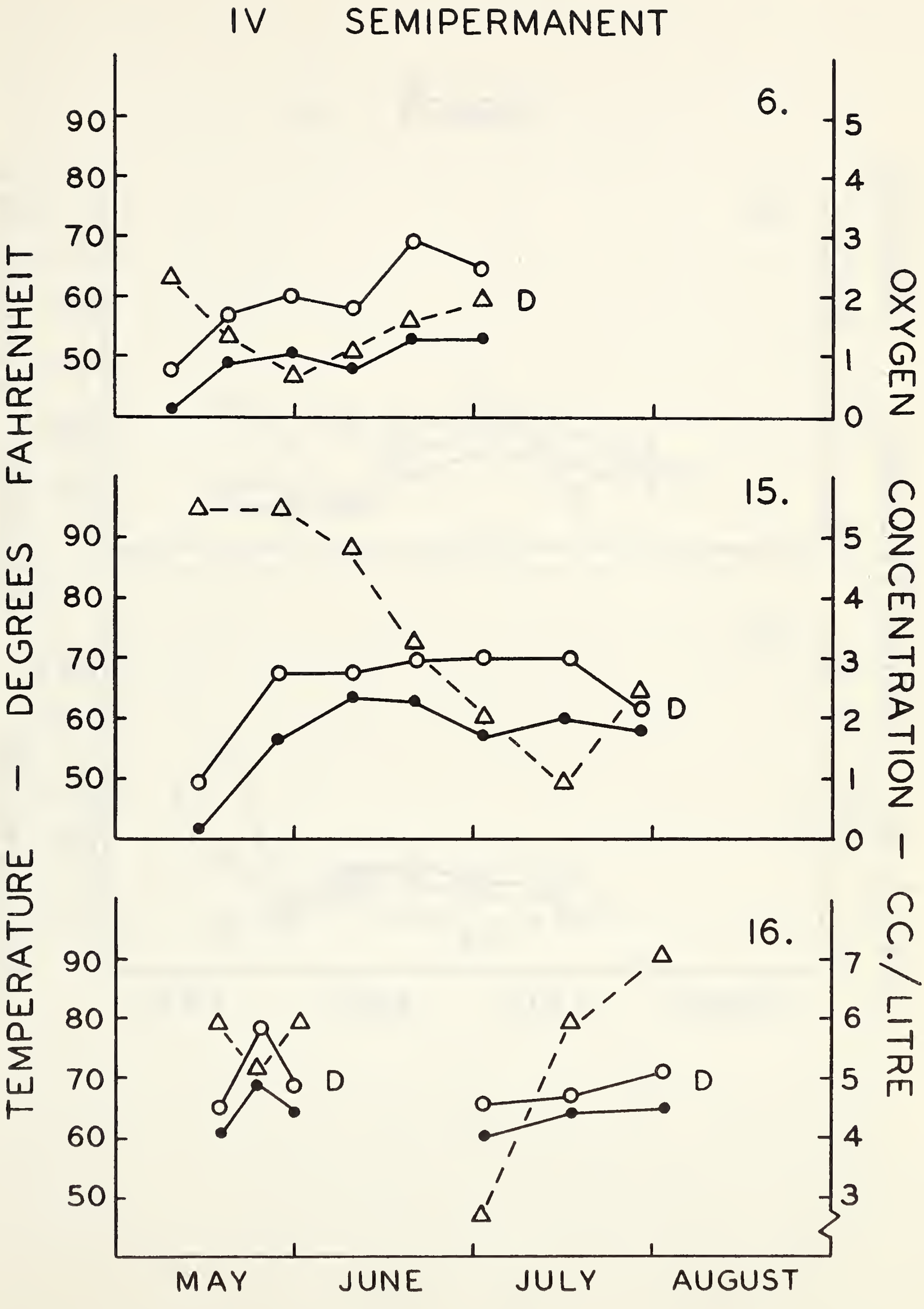

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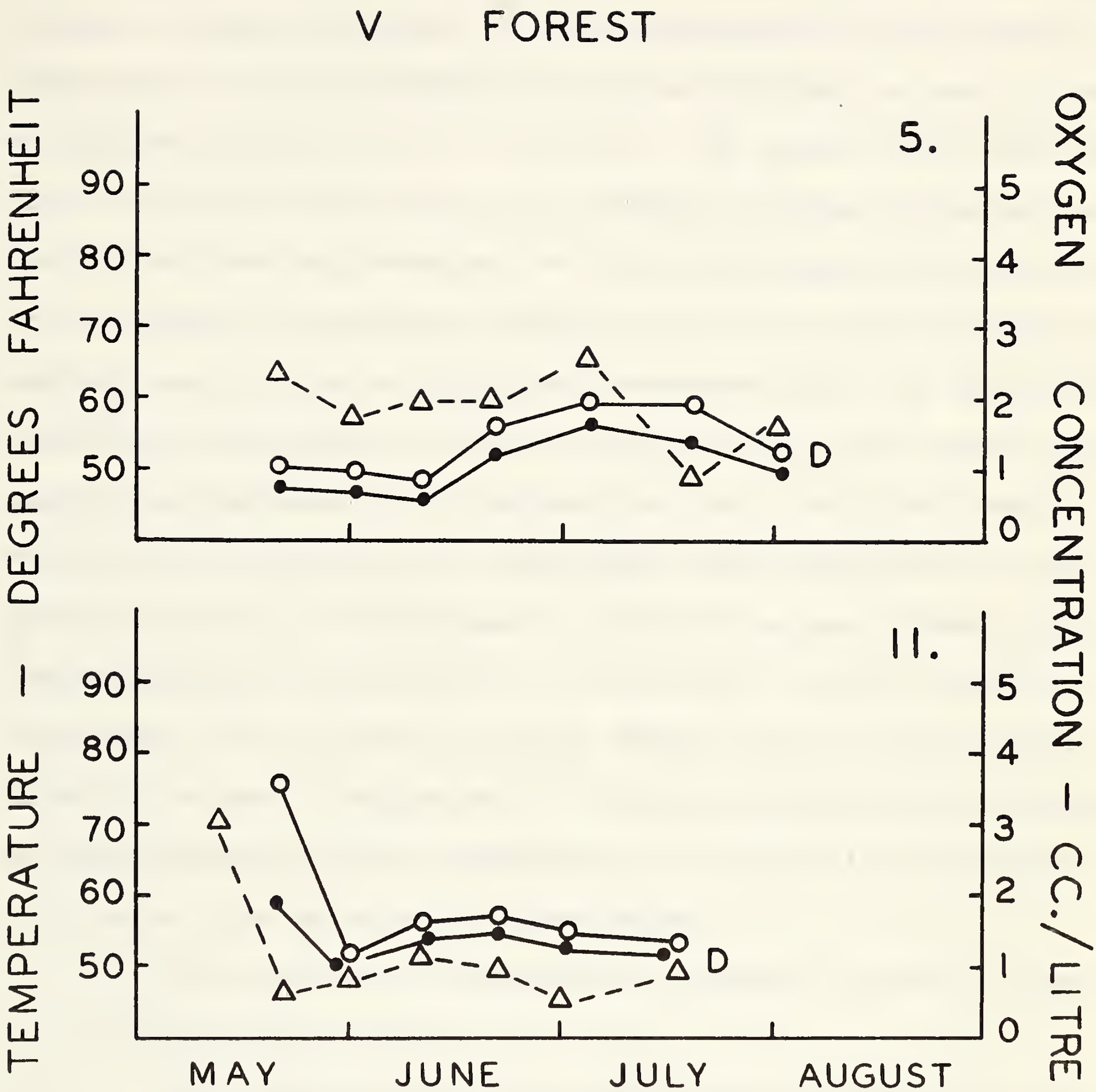


Fig. 14 (continued)

oxygen concentration could be expressed as percentage saturation; the same absolute amount of oxygen would then give different percentage readings depending on the temperature of the water.) The water for the estimation was collected from as near to the surface as possible (2 to 3 inches). The graphs (Fig. 14) show that in all habitats there is a gradual decrease in oxygen concentration from May onwards, the rate depending on the habitat. This decrease is expected because of the increasing temperature and increasing rate of biological decomposition. In protected locations, regardless of their classification, the oxygen concentration decreased and remained low throughout the summer (Locations 7, 8, and 13). Where open water was present, wind action resulted in turbulence so that the oxygen concentration increased again (Locations 2, 12, and 14). At this time in the summer, the biological oxygen demand would be decreasing allowing oxygen to accumulate. This may explain why reflooding of a dry habitat in July (Locations 10 and 16) is accompanied by a rapid rise in oxygen concentration.

The pH of all the habitats remained between 5.0 and 6.5 throughout the summer.

The temperatures and oxygen concentrations for 14 locations are plotted in Fig. 14. It is doubtful if these factors directly affect the mosquito larvae. Certain water conditions are associated with certain habitats, and there are certain associations between mosquito species and habitat types (Table 3), but any correlation between mosquito species and the water conditions is probably not significant. The behaviour of

the female mosquito towards the environment is more important in determining species distribution between the habitats. It will be shown in Section 3.4 that mosquito larvae can develop in any of the habitat types regardless of where the larvae are found in nature.

These graphs (Fig. 14) show that mosquito larvae can tolerate a wide range of water conditions. Most *Aedes* larvae have completed their development by the end of May, and when *Anopheles*, *Culex*, and *Culiseta* species develop later in the season, temperatures are higher, oxygen concentration is more variable, and associated animals are less numerous. The conditions of the water affect the larvae in four ways:

1. The date when the snow melts partly determines the date when hatching takes place. This varies from species to species, and from pool to pool (Fig. 13).

2. The temperature of the water in the habitat determines the speed of development of mosquito larvae. In a cold year the period between first and last emergence is prolonged.

3. A small snow fall in the winter, and rapid drying of the habitats can result in competition between larvae, and between larvae and other aquatic organisms. This competition may have an effect on the subsequent adult population (Irwin, 1942; Surtees, 1959). In 1961, several pools were found where the water had evaporated and seeped away leaving the larvae of *A. communis* stranded on the moist substrate.

4. Oxygen concentration of the water does not affect

the mosquito larvae directly since they breathe air at the surface. However, low oxygen concentrations, less than 2.0 cc/l., limit the populations of other aquatic animals including possible predators on mosquito larvae. Thus competition for space and food is minimized. Table 9 shows the aquatic animals associated with mosquito larvae, and that few are associated with larvae in forest pools.

3.3 Abundance of Larvae

Mosquito larvae were collected at each visit to a habitat. The sample was the number of mosquito larvae collected in one dip with an 800 cc. dipper; at each visit three samples were taken and the average numbers of larvae per sample are plotted in the histograms (Fig. 15). This method is liable to serious error because of the environmental variations within each location. Some areas of a pool, for instance the grassy fringe of a pool, will have a high density of larvae while the open water may have no larvae. The abundance recorded for each location depends on where the sample was collected. Larvae may occur in a particular region of a pool because of the light intensity and the temperature variations in the water (Haufe, 1957); this is very noticeable in forest pools. To overcome these difficulties, samples were only taken in regions where larvae were known to be present. So it is not possible to conclude from the histograms that a habitat *in toto* has the largest population; it may have the

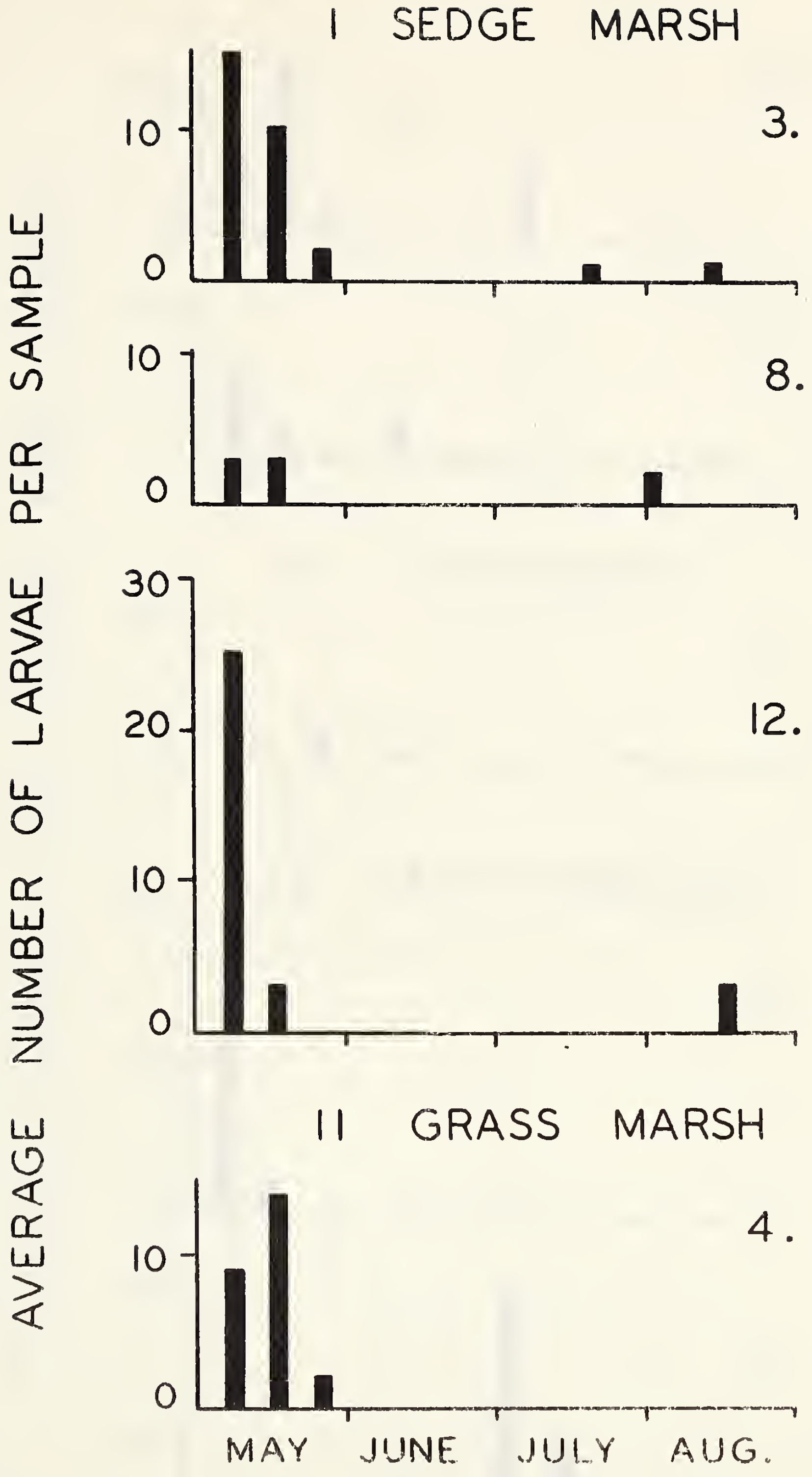


Fig. 15. Histograms of larval abundance, 1961, for the five habitat types. No mosquito larvae were found in locations 7 (semipermanent), 9, and 14 (permanent).

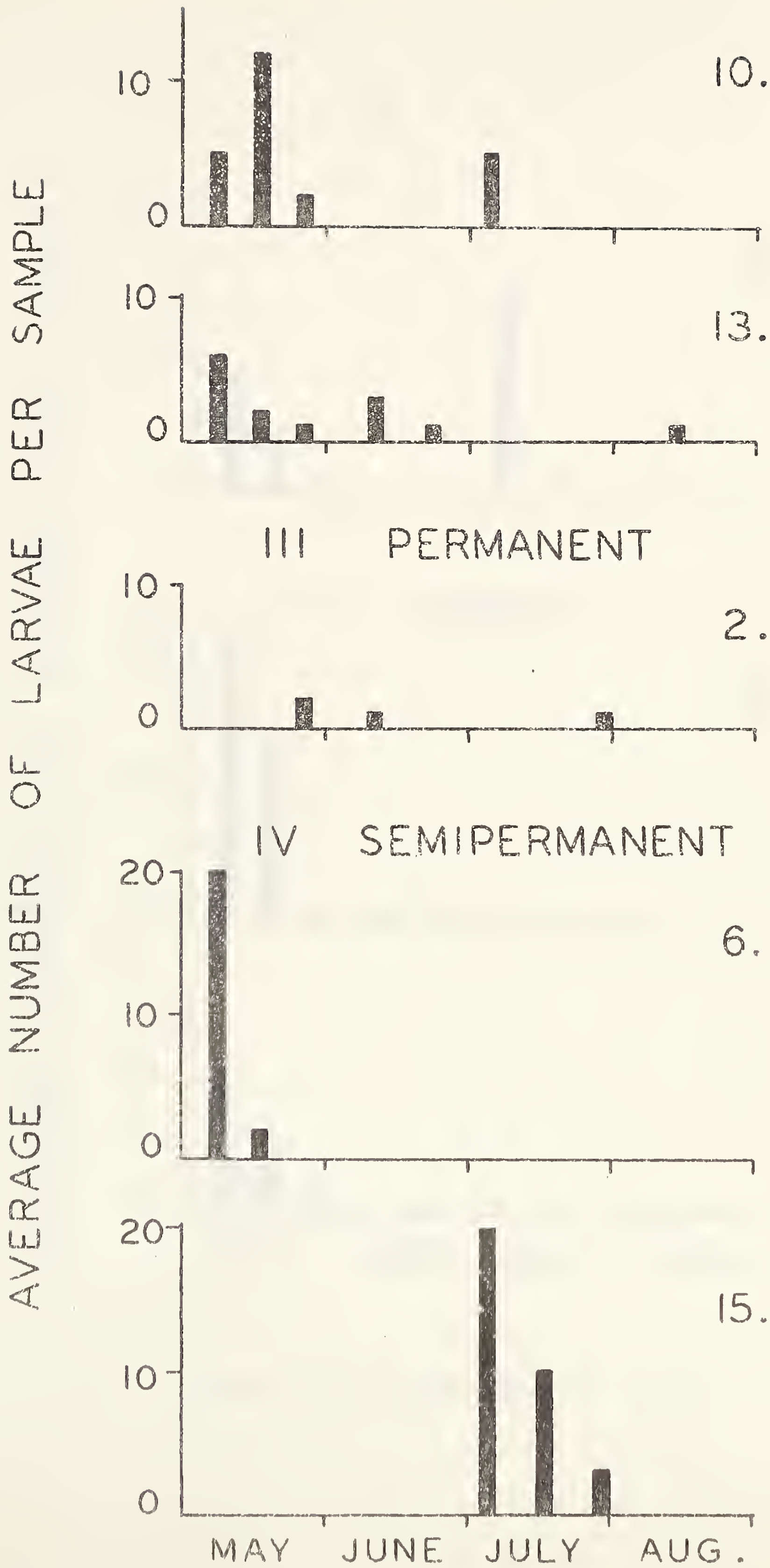


Fig. 15 continued.

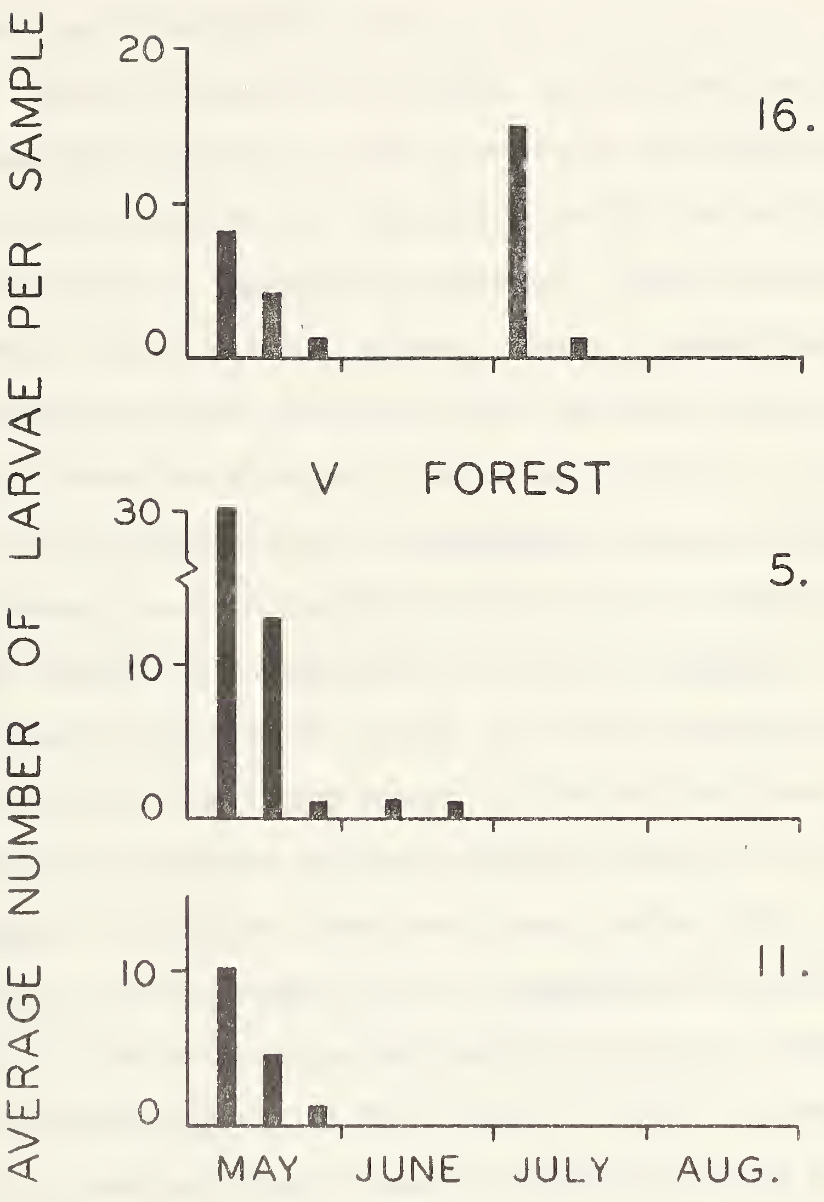


Fig. 15 continued.

highest density in the region where larvae were found, but another habitat, because of its uniformity, may have an overall higher population. Larvae collected in these samples were preserved and identified later.

The histograms are based on the 1961 collections. The population density in most locations is highest in early May; there is a decrease in density until the end of the month by which time most *Aedes* have emerged. Sedge marshes contain the highest densities of larvae. Grass, semipermanent, and forest habitats have lower and more variable densities, and no *Aedes* larvae were found in permanent waters. In July and August, small populations of *Anopheles*, *Culex*, and *Culiseta* species were found in habitats which had not dried up, but never in densities comparable to those of *Aedes*. The high populations at locations 15 and 16 at the beginning of July are a result of the heavy rains at the end of June which reflooded the habitats causing another brood of larvae, mainly *A. vexans*, to develop. Whether these larvae were a second generation - it is known that *A. vexans* can be multivoltine - or whether they were from eggs which failed to hatch in the spring (Gjullin *et al.*, 1950; Rempel, 1953) is unknown. When the adults emerged they formed a population peak higher than at any previous time in the summer.

The results from the 1962 collections were similar except for certain details:

1. The average number of larvae in all samples was only about half that of 1961 yet the adult population graphs

(Figs. 18 and 19) show that there was nearly double the number of adult mosquitoes compared with 1961.

2. There were no second broods in 1962. Habitats remained under water until late July and August.

3. The snow melt waters warmed up quicker in 1962 than in 1961. Emergence was up to a week earlier in 1962.

4. Anopheles earlei larvae were found from mid-May to the end of July in 1961, but only in late July and August in 1962 (Fig. 13). In both years larvae appeared a week or so before the adults disappeared. Culex territans and Culiseta spp. larvae were found over a longer period in 1961 than 1962.

Larvae of 22 species were found in the locations investigated, and their distributions are shown in Table 4. There is a considerable difference in each of the habitat types; grass habitats contained 16 species, sedge habitats 11 species, semipermanent waters 10 species, forest habitats 6 species, and permanent habitats 2 species. The most productive environment, the sedge marsh, is dominated by A. punctor, one of the most numerous species. A. communis, although abundant in forest waters, is also found in association with A. punctor. Most of the species found in the sedge marsh have been found at some time in grass habitats in small numbers. A. riparius and A. excrucians are the most abundant species in grass marshes, A. vexans, A. cinereus, and A. punctor are not uncommon. The principal species in this habitat are those that are most frequently encountered in the open as adults. Some species which are not found elsewhere, for example Culiseta spp., are

TABLE 4

Mosquito Species breeding in the Study Area showing Habitat Distribution. XX = found abundantly; X = found occasionally

Species	I Sedge	II Grass	III Semi-Permanent	IV Permanent	V Forest
Aedes cataphylla		X			
Aedes cinereus		XX			
Aedes communis	X				XX
Aedes diantaeus	X		X		
Aedes excrucians	X	XX			X
Aedes fitchii		X	X		
Aedes flavescens			X		
Aedes implicatus	XX	X	XX		X
Aedes intrudens		X	X		
Aedes pionips					X
Aedes punctor	XX	X	X		X
Aedes riparius	X	XX	X		
Aedes spencerii		X			
Aedes sticticus	X		X		X
Aedes trichurus		X			
Aedes vexans	X	XX	XX		
Anopheles earlei				X	
Culex territans	X	X	X	X	
Culiseta alaskaensis		X			
Culiseta impatiens		X			
Culiseta incidens	X	X			
Culiseta morsitans	X	X			
TOTAL:	11	16	10	2	6

found here also. Species typical of sedge and grass habitats are found in semipermanent waters as well.

Aedes communis is mainly found in the forest habitats; in many places it was the only species found in a pool. Location 15, a mixture of forest and sedge marsh habitats, was the only place where *A. pionips* was found. *Anopheles earlei*, *Culex territans*, and probably *Mansonia perturbans*, breed in the permanent waters of the lakes, a habitat which produces fewer mosquitoes than any other in the study area; no larvae were found in two out of the three locations of this habitat type.

The commonest species, *A. excrucians*, *A. punctor*, *A. riparius*, *A. vexans*, were found in most locations. The forest pools provide many breeding places for *A. communis*. The other species are more restricted in the places where they will breed; this may be one of the reasons why they are less common.

Some authors (*e.g.* Natvig, 1948) have published charts indicating the associations of larvae of different species in a pool or location. Table 5 shows the number of times when two species were found living in the same patch of water at the same time. All species, except *Culiseta impatiens*, were found in association with one or more other species; the most abundant species, which are also the least selective in their breeding habitat, were found in association with the largest number of other species, *e.g.* *A. excrucians*, *A. punctor*, *A. riparius*, and *A. vexans*. The numbers on the diagonal (under-

TABLE 5

The Associations of larvae. Each number shows the number of times two species were found together. The numbers on the diagonal (underlined) show the number of times a species was found alone.

Species	A. cataphylla	A. cinereus	A. communis	A. diantaeus	A. excrucians	A. fitchii	A. flavescens	A. implicatus	A. intrudens	A. pionips	A. punctor	A. riparius	A. spencerii	A. sticticus	A. trichurus	A. vexans	Culex territans	C. alaskaensis	C. impatiens	C. incidens	C. morsitans	Anopheles earlei
A. cataphylla		1		1	1			1				1		1								
A. cinereus	1			1	3	3	1	1	1			3		2		4					1	
A. communis			1	4	4			6	1	2	8	2		2		1						
A. diantaeus	1	1	4		1	1		2	1	3	5	2		2		2						
A. excrucians	1	3	4	1	3	1	1	2	1	1	2	2		8		4	1			1		
A. fitchii		3		1	1	1	1			1		3		2		4						
A. flavescens		1			1	1		1	1		1	2		1		3						
A. implicatus	1	1	6	2	2			1	1	1	7	8	2	3		2						
A. intrudens	1		1	1	1		1	3		1	2	4	1	2		3					1	
A. pionips			2	3		1		1	1	4	1	2		2		3						
A. punctor			8	5	2		1	7	2	1	4	9	1	1		3					1	1
A. riparius	1	3	2	2	1	4	2	8	4	2	9		2	4	1	10					1	1
A. spencerii								2	1		1	2			1	1						
A. sticticus	1	2	2	2	8	2	1	3	2	2	1	4		6		5	1			1		
A. trichurus												1	1									
A. vexans		4	1	2	4	4	3	3	2	3	3	10	1	5		3						
Culex territans					1								1				10	2		5	1	3
C. alaskaensis																	2	1		1	1	
C. impatiens																			1			
C. incidens					1									1			5	1		1		
C. morsitans	1							1			1	1					1	1			1	
Anopheles earlei											1	1				1	3					3

lined) in Table 5 indicate the number of times a species was the only one occurring in a location; except for Culex territans, this is exceptional. This Table shows that there are associations of different species of the same genus, probably because selection of the habitat by the female mosquito is independent of females of other species. This has no undesirable effects because of the temporary nature of the larval stage.

3.4 Rearing Cages and Transplant Experiments

To supplement the collections of larvae, rearing cages were placed in some of the habitats. These cages covered one square foot of water surface, were two feet high, and covered with nylon mosquito netting. Legs projected two to three inches from the bottom of the cage so that it could be fixed to the substrate, although the spongy moss often made this difficult. The top had a detachable lid; this was left off the cage until the first pupae appeared, so that heat gain during the day and heat loss at night would not be affected. Adults were collected at intervals so the productivities of the habitats could be compared. The cages were given the same numbers as the locations but these were written in Roman numerals; for example location 3 contained Cage III and location 16 contained Cage XVI. The cages were placed quickly but carefully into the water so as to include all the larvae in that section of the water.

Table 6 shows the number of Aedes mosquitoes that

TABLE 6

Aedes adults emerging into rearing cages, 1961

Cage	Males	Females	Total	Habitat
I	0	0	0	Forest
III	30	18	48	Sedge
IV	2	3	5	Grass
V	140	144	284	Forest
X	8	7	15	Grass
XII	35	33	68	Sedge
XVI	124	26	150	Semi-permanent

TABLE 7

Analysis of water from habitats where larvae were transplanted:

23 May, 1962

Expressed as parts per million

	Locations				
	2	3	4	11	16
p.p.m.	Permanent	Sedge	Grass	Forest	Semi-Permanent
Total Solids	286	186	1136	438	198
Ignition loss	150	118	118	252	140
Hardness	185	95	95	360	100
Sulphates	28	14	553	11	10
Chlorides	nil	1	1	2	1
Alkalinity	155	75	65	290	70
Nature of alkalinity - Bicarbonate of lime and magnesium					
Nitrites	nil	nil	nil	nil	nil
Nitrates	nil	nil	nil	nil	nil
Iron	0.6	0.2	0.2	trace	0.3

emerged into the cages in 1961, most of them in late May. The expected 1:1 sex ratio was approximated in all cages except cage XVI. A chi-square test on the results from cage III shows that there is no significant difference between the observed results and the theoretical 1:1 ratio at the five per cent level. Since males generally emerge before females, the female population will be reduced if the habitat dries up. This tends to give a preponderance of males, *e.g.* cage XVI.

Table 6 also shows that the sedge habitats and semi-permanent waters are the most productive ones. The large number of mosquitoes from cage XVI is mainly the second brood of *A. vexans*. The results from cage V need some explanation; the water was cold (40 - 55°F) and the oxygen concentration was low, there was little light, and few other animals were living in the water. Development was slow and emergence was spread over a longer time than in other places, but there were no known adverse factors to affect the population. Hence the male to female ratio is extremely close to 1:1 (140:144).

There are some pools where certain species breed and others where they do not (Table 4). This could either be because no eggs are laid in some habitats, or because hatching stimuli are lacking, or because there is an early mortality. To resolve this, populations of larvae were moved from one habitat type and placed in a rearing cage in one of the other habitat types. The larvae were moved on 14 and 15 May 1962 when in the second and third instars. Thirteen transplants,

TABLE 8

The results of experiments on transplanting *Aedes* larvae from one habitat type to another. This Table should be compared with Table 4.

Habitat of origin	Habitat where emerged: Sedge	Grass	Semi-Permanent	Permanent	Forest
Sedge	--	*cinereus* *excrucians* *riparius*	*cinereus* *punctor*	*communis* *diantaeus* *intrudens* *punctor*	
Grass	*cinereus* *implicatus* *punctor* *riparius*	--	*punctor*	*cinereus* *punctor*	*communis* *excrucians* *punctor*
Semi-permanent	*intrudens* *punctor* *riparius*	*communis*	--		*communis* *intrudens* *punctor*
Permanent	No *Aedes* larvae are indigenous in permanent habitats				
Forest	(*riparius*)			*communis*	--

each of an estimated 30 to 40 <u>Aedes</u> larvae, were made as shown in Fig. 16.

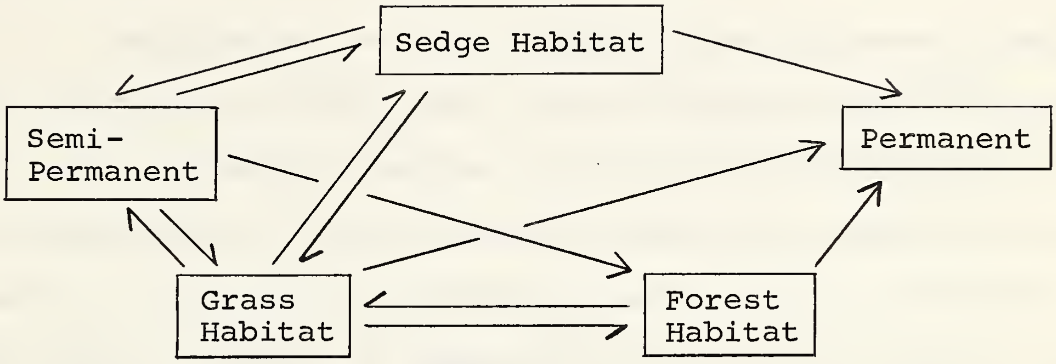


Fig. 16. Scheme to show how larvae were transplanted.

The cages were placed in a part of the habitat where there were few, if any, indigenous larvae. Consequently adults emerging into the cages were mostly from transplanted larvae. However, when <u>A. communis</u> emerged into the forest cage where the grass habitat larvae were transplanted, it is certain that these specimens were from indigenous larvae since <u>A. communis</u> does not breed in grass habitats. Mosquitoes emerged into all cages regardless of their position or the origin of the larvae (Table 8), although some transplants were more successful than others.

Samples of water collected on 23 May 1962 from the five habitats where larvae were transplanted were analysed for their chemical constituents (Table 7). Total solids were much higher at Location 4 (grass habitat) but even this figure was lower than anticipated for this time of year. Sulphate

was fifteen times higher at this location than elsewhere, while the highest alkalinity, corresponding to a pH of about 8.0, was found in the forest location (11).

Another set of water samples from the same locations was collected on 28 June 1962. Most readings were different from those in the May samples. As the water evaporates salts are concentrated. Thus during the summer, the chemical components of the water vary greatly, particularly in habitats which dry up. Larvae of Aedes are mainly found in April and May when less evaporation occurs and conditions are relatively more stable. However, Aedes larvae may be found in waters of varying chemical constitution, and they can develop within the range of conditions shown in Table 7. Rapp (1960) has given the chemical composition for three habitats and shown that mosquito larvae can live in a wide variety of chemical conditions; he concluded that certain species, including A. vexans, are not affected by high concentrations of inorganic salts.

3.5 Container Habitats

There are no naturally occurring container habitats where mosquitoes can breed in the study area. Twenty five old tins and enamel dishes filled with lake water were placed in the willow scrub and forest habitats at ground level, three feet, and six feet in July 1961 to see if mosquitoes would oviposit in them. Rainwater was insufficient to replace the water lost by evaporation but the containers did not dry up

completely. During the winter they were filled with snow, while additional snow formed caps above them. When the snow melted, most of the containers were full of water, and after a few weeks the water was stagnant and covered with scum. Mosquitoes were observed flying around the containers in both years, but no larvae were found in them in either year.

3.6 Effect of Snow and Ice on Larvae

In 1962, the heavy winter snow had melted in most places by the beginning of April. By the end of April, larvae were abundant. On 4 May 1962, twelve inches of wet snow fell, and the air temperature dropped reaching 20°F on the night of 5 May. For the next two days, the temperature was below freezing each night and did not rise above 50°F during the day. The surface of the water was covered by an inch of ice in places. The ice had intermingled with the loose snow, had melted, and refrozen to form a crystalline mat nine inches thick over the surface of the sedge marshes (Fig. 17). However, some water remained unfrozen among the clumps of dead sedge. Few larvae were seen when the snow and ice were removed. Some were found around the clumps of dead sedge, alive but inactive; others, for example _A. punctor_ and _A. implicatus_, were found dead under the ice. In the grass marsh (location 4) where the ice was unbroken, no larvae were seen.

Temperature readings taken at 1400 hours on 5 May in a sedge marsh, location 3, illustrate that there is some

Fig. 17. A sedge marsh (location 3) with rearing cages after the snowfall on 5 May 1962. The water is frozen on the surface except where clumps of sedge are covered with snow.

protection from the cold in the deeper water:

In snow	30°F
Water one inch deep flowing over ice ...	34 - 36°F
Water under ice	35 - 40°F
At margin of marsh, no ice	42°F

Larvae covered by ice appear to have been killed. Those in a sedge marsh, if they remained by a clump of dead vegetation, survived. Mosquito larvae in a sedge marsh have a greater chance of survival under these prolonged cold conditions, but since cold will reduce the metabolic rate, larvae may be able to survive for several days in any habitat without replenishing their air at the surface. No adverse effects of this cold period could be detected in the subsequent adult population.

3.7 Inter-relationships between Mosquitoes and other Aquatic Animals

Aquatic animals associated with mosquito larvae were collected on three occasions: 26 May 1961, 4 July 1961, and 19 May 1962. A list of the animals and the habitats where they were found is given in Table 9. Pennak (1953) was used to identify the animals.

In the spring when *Aedes* larvae were abundant, the animals in Table 9 were common but they rarely attained the numbers of the mosquito larvae. However, the collections at the beginning of July contained only snails, damselfly and

TABLE 9

Other animals associated with mosquito larvae in different habitat types

	Sedge				Grass			Permanent			Semi-perm.				Forest		
Location Number	3	8	12	17	4	10	13	2	9	14	6	7	15	16	1	5	11
Platyhelminthes																	
Turbellaria		X					X										
Annelida																	
Hirudinea		X								X		X					
Oligochaeta							X										
Crustacea																	
Anostraca																	
Chirocephalidae		X				X			X			X		X			
Ostracoda																	
Daphnia sp.	X	X	X	X	X	X	X		X	X			X	X			
Copepoda																	
Cyclops sp.	X			X		X	X										
Amphipoda																	
Gammaridae										X	X						
Insecta																	
Odonata																	
Anisoptera					X			X	X	X		X					
Zygoptera																	
Coenagrionidae									X			X			X		
Coleoptera																	
Dytiscidae larvae	X	X	X	X	X	X	X		X	X	X		X	X	X		X
Hydrophilidae l.												X					

(continued)

TABLE 9 (continued)

Location Number	Sedge 3	8	12	17	Grass 4	10	13	Permanent 2	9	14	Semi-perm. 6	7	15	16	Forest 1	5	11
Insecta																	
Coleoptera - con'd.																	
Dytiscidae adult																	
Ilybius sp.			X														
Hygrotus sp.			X														
Hydraporus sp.						X	X	X		X			X		X		
Agabus sp.													X				
Hydrophilidae ad.																	
Laccobius sp.		X							X	X							
Enochrus sp.									X								
Diptera																	
Tipulidae	X		X	X						X							
Syrphidae																	
Eristalis sp.					X												
Culicidae																	
Eucorethra										X							
Mochlonyx	X	X	X		X	X	X				X			X		X	X
Dixidae											X						
Chironomidae											X				X		
Trichoptera																	
Limnephilidae																	
Glyphotaelis sp.	X		X			X			X	X				X	X	X	
Limnephilus sp.			X		X				X				X	X			
Hemiptera																	
Corixidae		X	X				X		X	X		X			X		

(continued)

TABLE 9 (continued)

	Sedge				Grass			Permanent			Semi-perm.				Forest		
Location Number	3	8	12	17	4	10	13	2	9	14	6	7	15	16	1	5	11
Arachnida																	
Hydrachnidae			X			X	X										
Mollusca																	
Lamellibranchiata		X	X											X			
Gastropoda																	
Planorbidae	X		X		X	X		X		X	X				X		
Lymnaeidae		X	X	X	X	X			X	X		X	X	X	X		
Physidae	X	X	X			X					X		X		X		
Amphibia																	
"Tadpoles"							X							X			

dragonfly nymphs, and water bugs. Most mosquito larval habitats had dried up by early July in 1961. Only the permanent waters and grass marshes still contained water. Copepoda and Cladocera were found throughout the summer. In contrast, fairy shrimps (Chirocephalidae) were very short lived; in 1961 they were found only in one grass marsh (10) where they were more numerous than mosquito larvae, but they had died by mid May. Most aquatic larvae of insects emerged by early June.

Table 9 shows that some species have a wide distribution. The predatory Mochlonyx velutinus (Ruthe), Cladocerans, Copepods, caddis fly larvae, corixids, larval and adult dytiscid beetles, and snails were common and found in many habitats. In contrast, other species were generally found in particular habitat types:

Chirocephalidae in grass and semipermanent habitats, Odonata in permanent habitats, larval Tipulidae in sedge habitats, and Eucorethra underwoodi Underwood in sheltered permanent water. Since certain mosquito species are associated with particular habitats, the aquatic animals with a limited distribution can be used as a guide as to which mosquito species, if any, are likely to be present.

Sedge, grass, permanent, and semipermanent habitats contain many aquatic organisms, whereas forest habitats only contain dytiscid beetles, Mochlonyx, and snails. Several factors may account for the less diverse animal life in forest pools: the oxygen concentration is lower than in other habitats; there is less light and hardly any vegetation, and the

water remains cool and dries up quickly.

Sedge and grass habitats contain the greatest variety and number of aquatic organisms; they also contain the greatest number of mosquito species (Table 4). Semipermanent and permanent habitats are also rich in animal life, but the latter habitat does not contain Aedes larvae. Forest pools contain few aquatic organisms. All these animals are adapted to temporary pools; either the life history is short, or only the larval stage requires an aquatic habitat, or if the adults are aquatic they can migrate to another pool.

It is not known how other aquatic organisms affect the mosquito population. Many authors have said that predation on mosquito larvae is an important factor limiting their numbers, but there is little evidence to prove it. In May, Aedes larvae are the most evident aquatic animals in all the principal breeding habitats. Predation cannot be called a limiting factor for these populations; if it does occur, it would be greatest in sedge, grass, and semipermanent habitats and least in forest habitats.

However, the work of Baldwin, James and Welsh (1955) and James (1961) has shown that many organisms do prey on mosquito larvae, although the extent of this is unknown. These authors released radioactive Aedes larvae into temporary pools, and 24 hours later they collected all the other aquatic organisms which were then tested for radioactivity. Some of the animals recorded as predators by these authors have been collected in the study area; for example Corixidae, Limnephilidae, adult

Dytiscidae (<u>Acilius</u>, <u>Agabus</u>, <u>Hydroporus</u>, <u>Hygrotus</u>) and adult Hydrophilidae (<u>Hydrobius</u>, <u>Hydrophilus</u>). James (<u>op. cit.</u>) concludes that "on the basis of their radioactivity and numbers, adults of Dytiscidae and of the Hydrophilid, <u>Hydrophilus obtusatus</u>, and the larvae of the caddis fly, <u>Limnephilus</u> sp., appeared to be the most effective predators of early instar <u>Aedes</u>". In the present study, species of Limnephilidae and Dytiscidae were among the commonest aquatic organisms.

Probably more important than predation is intra-specific competition which if severe can result in a smaller adult population. Surtees (1959) has shown experimentally that mortality in <u>Aedes aegypti</u> larvae is highest when there is a high population density. Competition for space is important in a dry year; where a moss mat forms tussocks, larvae may be isolated in patches of water as the water level subsides. Dead larvae have been found after a pool dried up in 1961.

4. RELATIONSHIPS BETWEEN MOSQUITOES AND DRAGONFLIES

4.1 Larvae

Dragonfly nymphs have been reported as important predators of mosquitoes (e.g. Barr, 1958; Bird, 1961; McClure, 1943). Dragonfly nymphs prey on mosquito larvae if they are placed in the same container; but this does not mean they have the opportunity to attack mosquito larvae under natural conditions. Table 9 shows that anisopteran nymphs were found in the permanent habitats where *Aedes* larvae do not breed. The nymphs in the grass and semipermanent waters were found later in the summer since they hatched from eggs laid in the spring; by the time these eggs hatched, the *Aedes* mosquitoes had emerged. Both habitats normally dry up, so no dragonfly nymphs would survive to prey upon mosquito larvae the following year. Since the nymphs overwinter before completing their life cycle, permanent waters are essential for their survival. Consequently *Aedes* larvae and dragonfly nymphs are temporally and spatially separated, so that little predation occurs.

Anopheles and *Culex* larvae are found later in the summer in some dragonfly habitats (Table 9) so predation by nymphs on these genera is more likely. Pritchard (1963), working in the same study area, found that 18 per cent of the dragonfly nymphs collected in June and August 1962 from habitats where *Anopheles* and *Culex* were present, contained remains of larvae. Neither of these genera are abundant in the study area.

4.2 Adults

Adult dragonflies and mosquitoes fly at different times. Dragonflies are active on sunny days when there is no dew and the saturation deficiency is high. As the temperature and light intensity drop, and the saturation deficiency decreases, dragonfly activity ceases, and the evening flight activity of mosquitoes begins. Although a few mosquitoes may be flying in the forests during the day, dragonflies tend to remain in the open and along the edges of the forest. It was common in June to walk along a path bordered with willow when mosquitoes were flying and biting in the early morning, and to find dragonflies clinging immobile to the vegetation. Later in the day, dragonflies were flying and no mosquitoes were active. Just before a daytime rainstorm as the relative humidity increases, mosquitoes and dragonflies fly at the same time; then predation may be considerable (Pritchard, *op. cit.*). As the humidity drops after the rainstorm, mosquito activity decreases although dragonflies are still active. In general, predation by dragonflies on mosquitoes is limited because they fly in different places, or when the weather is different.

Some adult female mosquitoes can tolerate, perhaps for only a short time, climatic conditions required by dragonflies for flight. *A. riparius*, *A. fitchii*, *A. punctor*, and *A. vexans* are the common species which, at different times of the season, can fly in the open during the heat of the day. The numbers flying under these conditions are small compared

with the numbers recorded at the morning and evening maxima. On 10 June 1961, a dragonfly, *Ladona julia* Uhler, used my arm as a base for 25 minutes while it was catching prey. Several times it took off and caught mosquitoes, mainly *A. riparius*, flying around me. It also caught caddis flies, and after each successful catch, the dragonfly landed on me again while still chewing its prey, often with part of the prey projecting from between its mandibles.

5. ADULT MOSQUITOES

5.1 Seasonal Fluctuations in Adult Population

Daily samples of the adult mosquito population were taken from 1 June - 26 August 1961 and from 25 May - 2 August 1962. Each sample was obtained in exactly the same locality; for most of the summer it was taken at 2000 hours, but as the days became shorter, the time was moved earlier to keep the sun time approximately the same.

The samples were caught by a standardized method on a small path passing through a large aspen forest (Fig. 3). The observer walked quickly up to the sampling point and immediately made ten sweeps with a net in five figures-of-eight encompassing a complete circle round himself. This sample was counted and recorded, but discarded. A second sample was captured in the same way and retained. The flight activity graphs and the conclusions drawn from them are based on this second sample which was usually slightly larger than the first. Biting rate, temperature at three feet above the ground, relative humidity, cloud cover, and wind speed were recorded at each sampling time. The flight activity graphs (Figs. 18 and 19) are taken as a measure of the mosquito population during the season (cf. Section 7).

Because of the daily variations in the weather, the number of mosquitoes in the samples fluctuated widely. To smooth this daily fluctuation so that the trend in the population could be studied, five day running averages were calculated. The numbers plotted are the averages of the

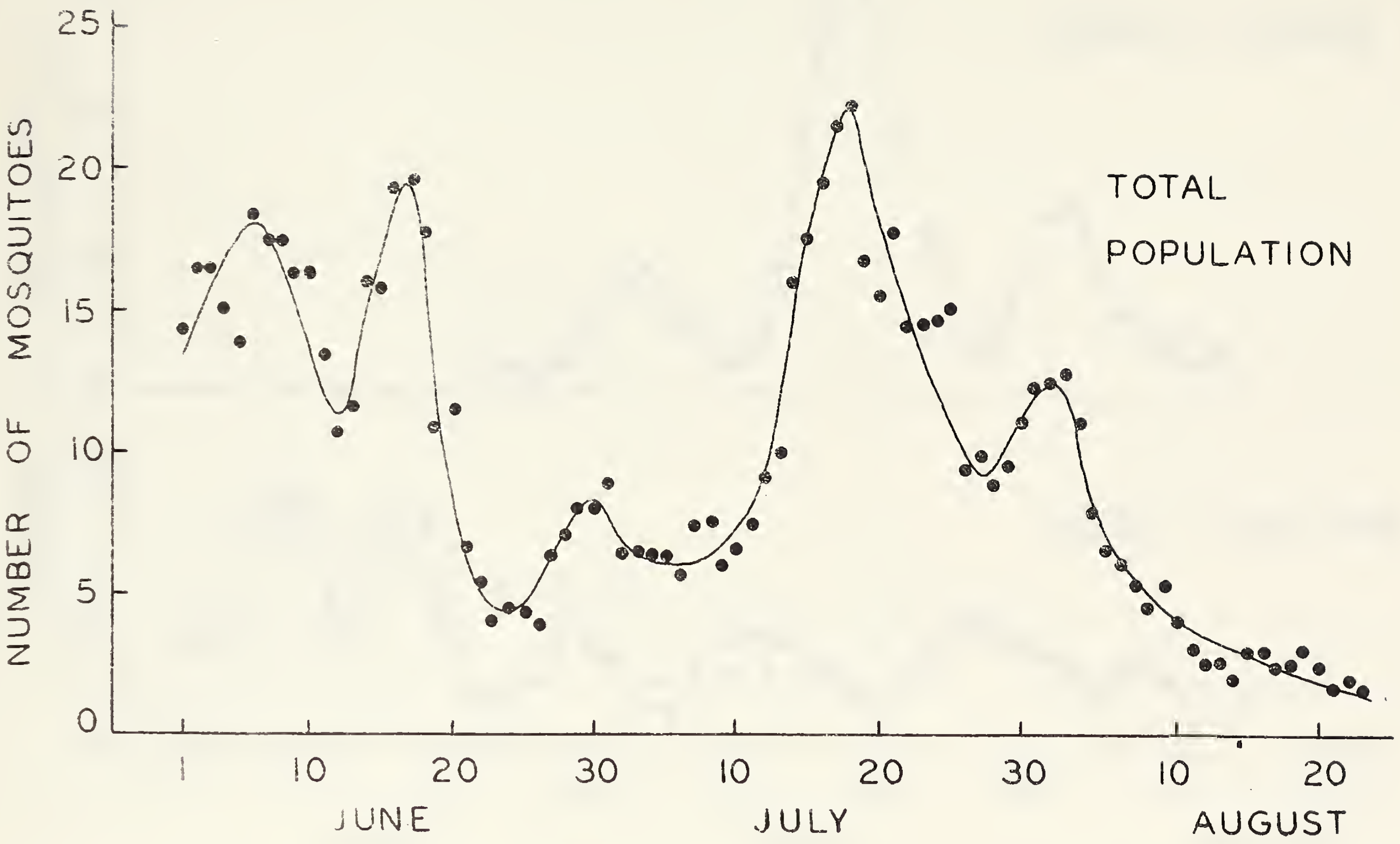


Fig. 18. Flight activity graphs, 1961, for the total mosquito population, and for *Aedes vexans*, *A. punctor*, *A. riparius*, and *A. excrucians*. The numbers of mosquitoes are plotted as five day running averages.

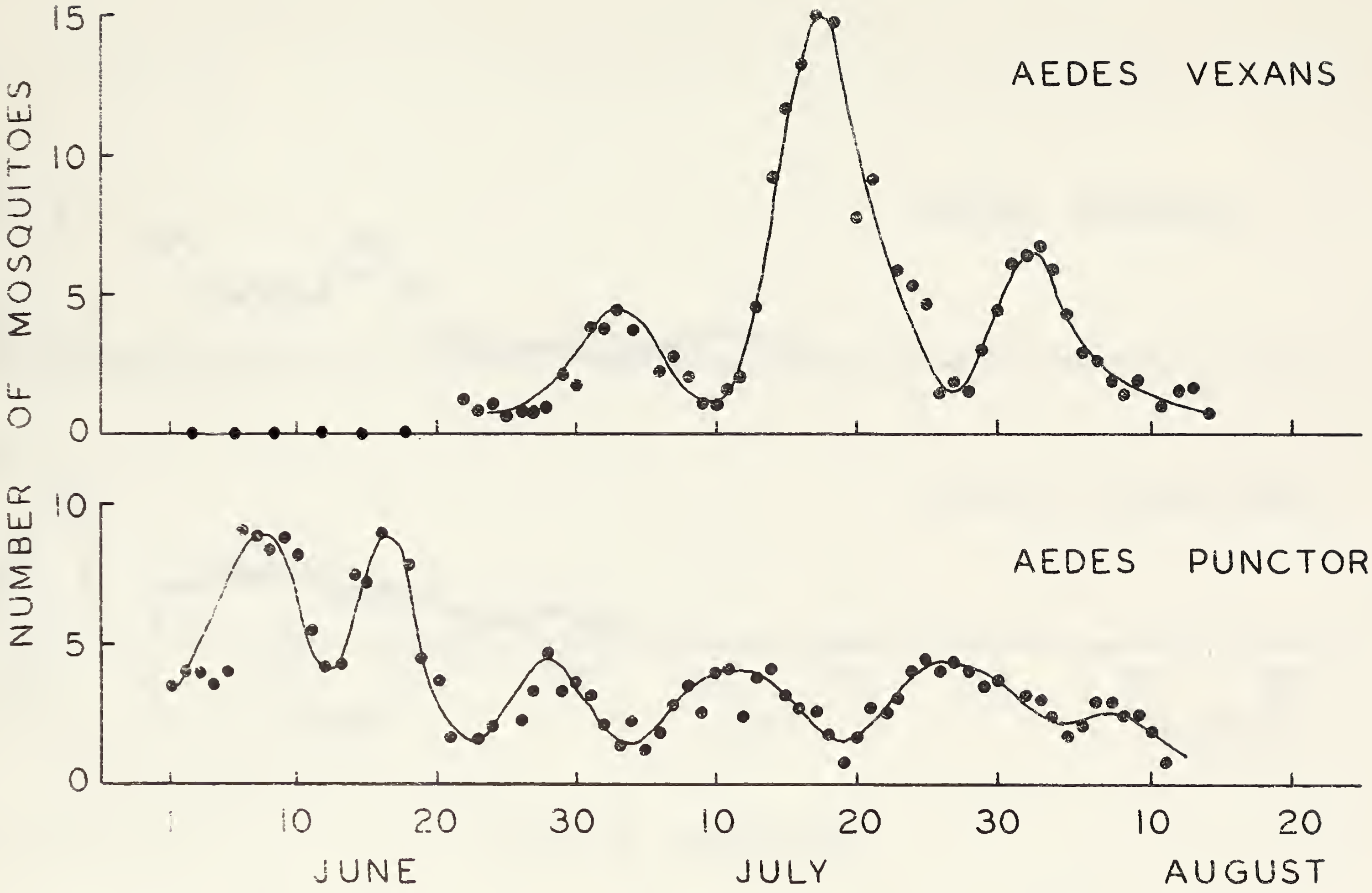


Fig. 18 (continued)

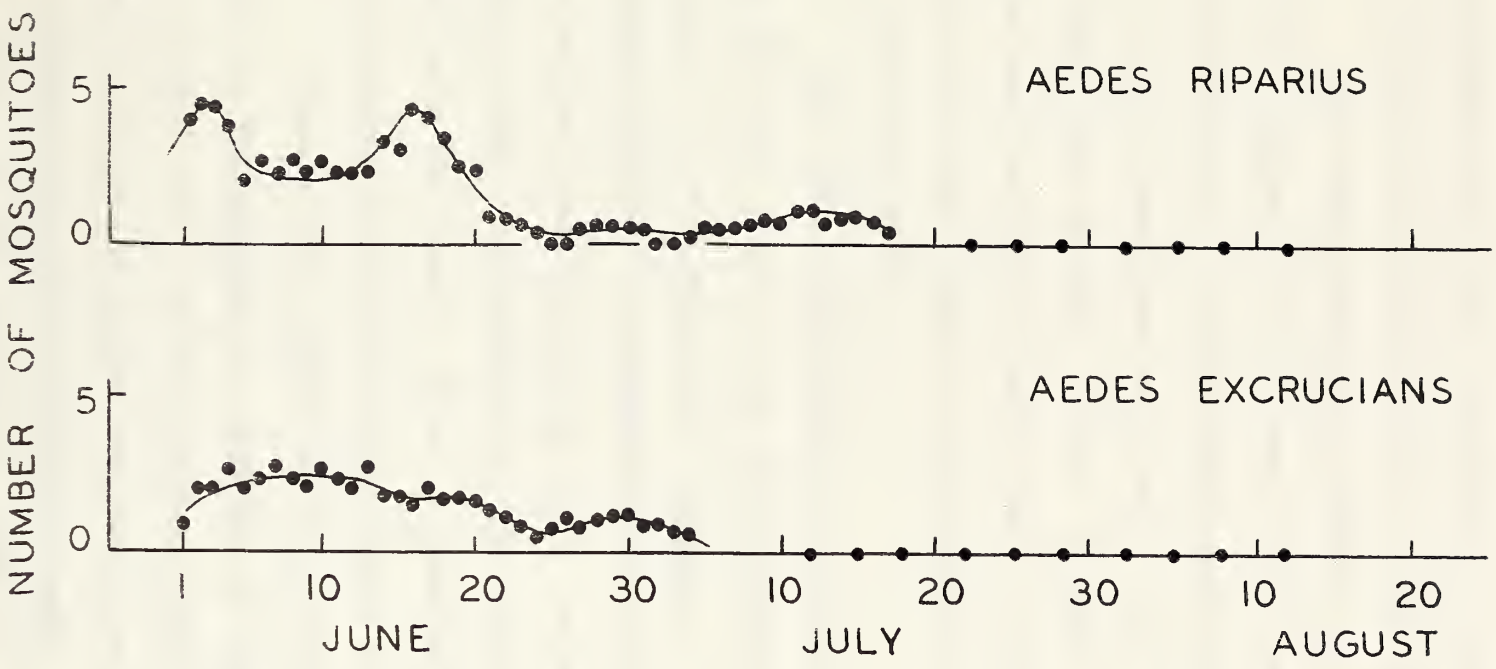


Fig. 18 (continued)

samples for five days; any particular day's sample modifies the average for five days beginning with the four days preceding it, and ending with the four days following it. This procedure does not eliminate long term weather effects which do cause real fluctuations in the population.

The most noticeable feature of the 1961 and 1962 population graphs is that there is no single rise and decline in the population. In 1961 there were five peaks of abundance while in 1962 there were only four. In 1961, 822 mosquitoes were caught and in 1962, 1,345. At one stage in 1962, the samples were more than double those at any time in 1961; the highest individual sample in 1961 was 36 mosquitoes, that in 1962 was 90 mosquitoes.

The 1961 population was modified by the heavy rains during the last week of June which reflooded some pools producing a second brood of *A. vexans*, so that the mosquito population started to increase on 10 July. In 1962, there was no second brood and by 18 July, the date of the greatest numbers in 1961, the population was declining rapidly and already at a low level. This is remarkable in view of the very high population less than a month previously.

Population graphs are also drawn for the most numerous species, *A. excrucians*, *A. punctor*, *A. riparius*, and *A. vexans* (Figs. 18 and 19). If the species graphs are superimposed on the total population graph, the peaks of certain species coincide with the total population peaks. Tables 10 and 11 show that some of the population peaks are the result of one

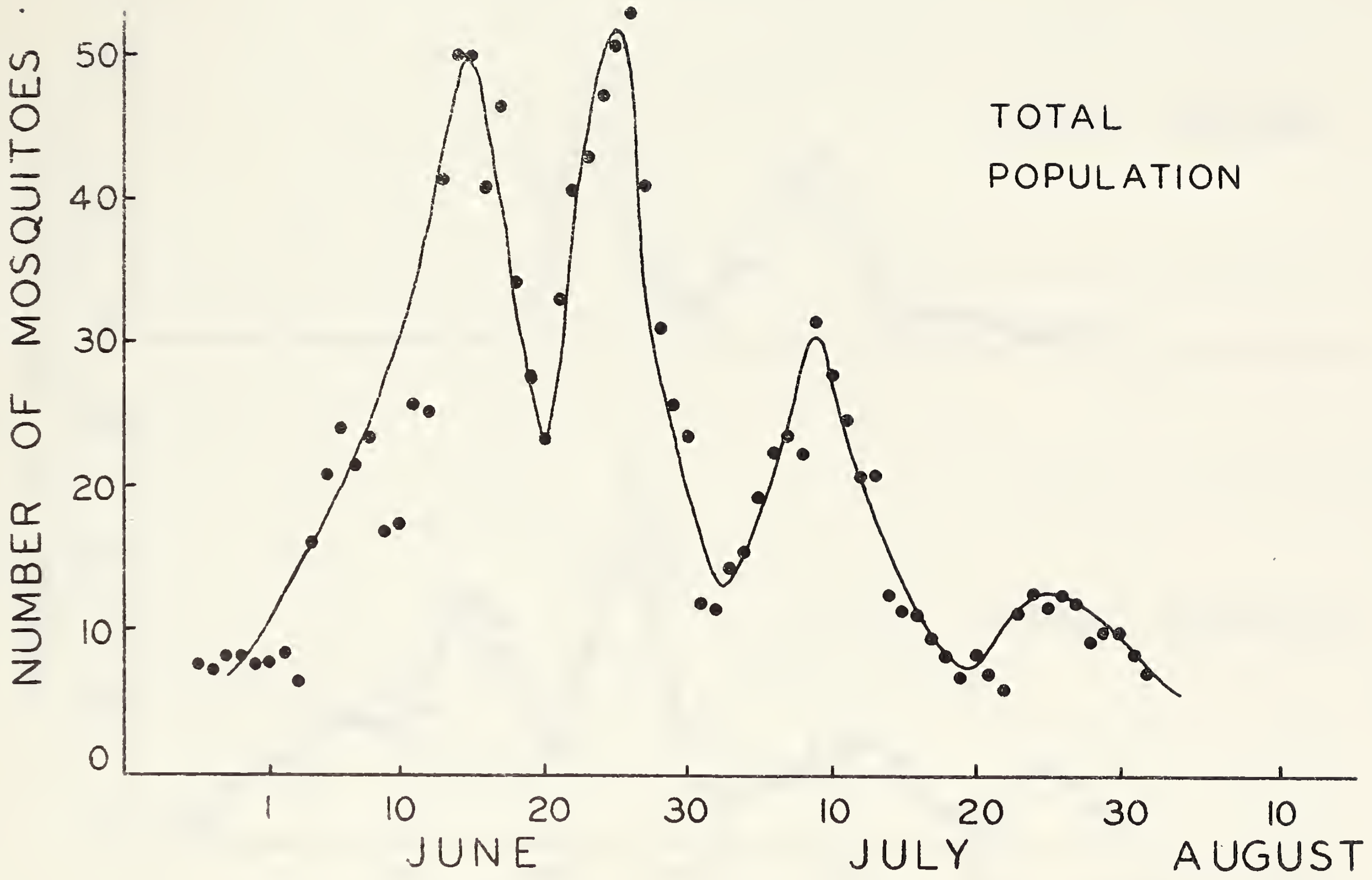


Fig. 19. Flight activity graphs, 1962, for the total mosquito population, and for _Aedes vexans_, _A_. _punctor_, _A_. _riparius_, and _A_. _excrucians_. The numbers of mosquitoes are plotted as five day running averages.

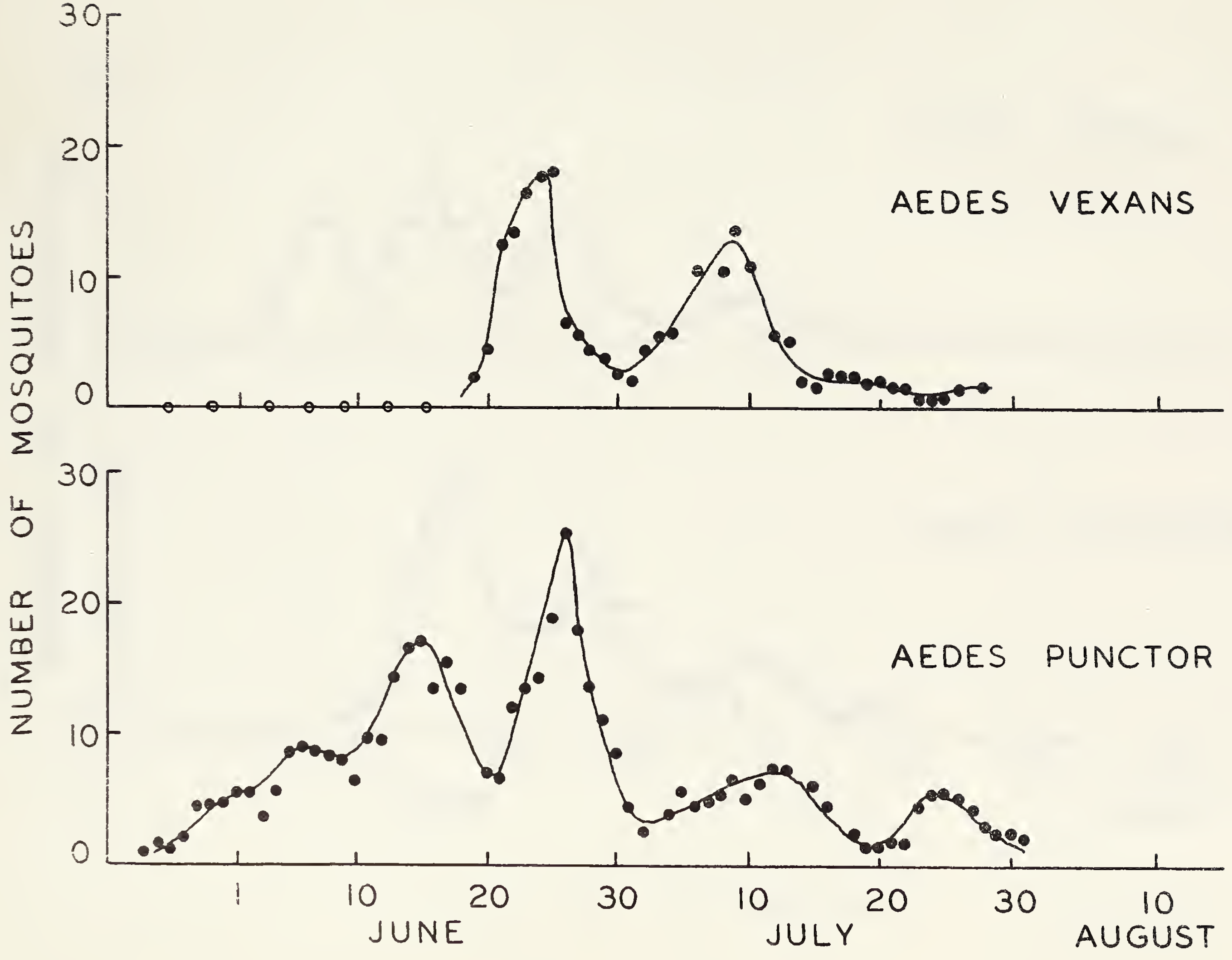


Fig. 19 (continued)

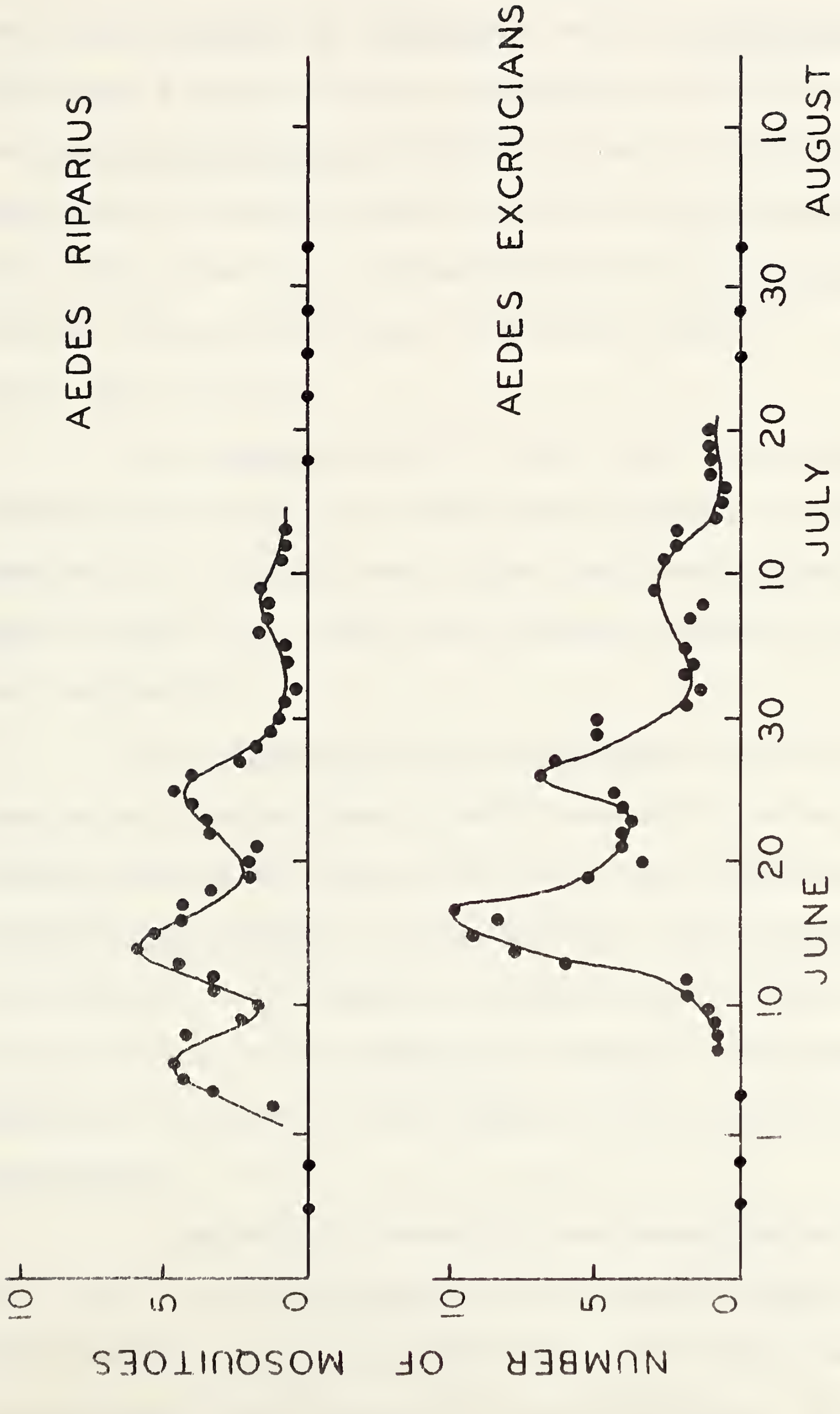


Fig. 19 (continued)

dominant species, and others are the result of more than one species.

In 1961 the population at the beginning of June was due to _A. punctor_, _A. riparius_, and _A. excrucians_. However, there was a drop in the _A. riparius_ population at the time of the _punctor-excrucians_ population peak (1); the _A. riparius_ population increased again to form the _punctor-riparius_ peak (2). From there on, the population of _A. punctor_ was at a low but fluctuating level with minor peaks on 29 June, 12 July, and 27 July.

A. vexans formed a small population peak with _A._ punctor on 1 July (3). The numbers making up the _A. vexans_ peak on 15 - 20 July were large, and they formed the highest peak in 1961 (4). There was another smaller _A. vexans_ peak on 3 August (5).

A. riparius and _A. excrucians_ showed similar population fluctuations. Both remained at a low level and neither lasted as long as the other main species. _Aedes cinereus_, _A. fitchii_, _A. implicatus_, and _A. intrudens_ were also present, but because of their small numbers, they had little effect on the population changes. Emergence of these species at the end of May added to the numbers of the initial population.

Graphs were drawn for the same species in 1962 (Fig. 19). As in 1961, the peaks of the species populations coincided with those of the population as a whole, and all but one of the peaks were formed by several species. _A. punctor_

contributed to all the population peaks (cf. 1961), and *A. vexans* to two of them. There was no second brood of *A. vexans* in 1962. *A. riparius* and *A. excrucians* showed several peaks of abundance. There was a peak of *A. riparius* on 5 June, and both species were partly responsible for the population peaks on 14 June, 26 June, and 9 July. Few remained by the fourth population peak in mid July. As in 1961, the numbers of the other species were small although *A. communis* was more numerous than in the previous year.

Both years showed several peaks of abundance, and the numbers at the beginning of the summer were due to the almost synchronized emergence of the *Aedes* species. The constituent species and the dates of the population peaks varied (Tables 10 and 11). The highest peak of *A. punctor* was on 15 June in 1961 but not until 25 June in 1962. In both years, the population was modulated by long term weather effects. *A. vexans* were first seen on 21 June in 1961, and they reached a peak on 3 July; the second brood resulted in two more peaks later. In 1962, the species was first seen on 19 June, and it reached a peak on 25 June. In 1961, the population of *A. excrucians* was low without any recognizable peaks, but in 1962 there were three definite peaks. *A. riparius* also showed definite peaks in 1962.

Table 12 shows the June and July results for 1961 and 1962. In 1962 twice as many mosquitoes were caught in this period (1256:638) but there is little difference in the percentages of each species in the two years. *A. punctor* was

TABLE 10

Constituent Species of adult mosquito population peaks, 1961

Peak	Date	Species
1.	6 June	*A. punctor*, *A. excrucians*
2.	17 June	*A. punctor*, *A. riparius*
3.	1 July	*A. punctor*, *A. vexans*
4.	18 July	*A. vexans*
5.	2 August	*A. vexans*

TABLE 11

Constituent Species of adult mosquito population peaks, 1962

Peak	Date	Species
1.	14 June	*A. excrucians*, *A. punctor*, *A. riparius*
2.	26 June	*A. excrucians*, *A. punctor*,
3.	9 July	*A. riparius*, *A. vexans*
4.	26 July	*A. punctor*

TABLE 12

Comparison of the total numbers of adult mosquitoes of six *Aedes* species captured in the forest samples, June and July, 1961 and 1962.

1961: 638 mosquitoes caught on 55 days

Species	Number caught	As % of total
A. communis	45	7.1
A. excrucians	51	8.0
A. fitchii	33	5.2
A. punctor	211	33.0
A. riparius	64	10.0
A. vexans	159	24.9
Remainder	75	11.8

1962: 1256 mosquitoes caught on 57 days

Species	Number caught	As % of total
A. communis	101	8.0
A. excrucians	137	10.1
A. fitchii	141	11.2
A. punctor	419	33.4
A. riparius	108	8.6
A. vexans	213	17.0
Remainder	137	10.9

the most numerous in both years. The percentages of *A. communis*, *A. excrucians*, *A. fitchii*, *A. riparius*, and *A. vexans* were lower and more variable. The second brood increased the percentage of *A. vexans* in 1961, and the percentage of *A. fitchii* in 1962 was double that in 1961. The way that the species population graphs merge or overlap determines the height and duration of the total population peaks.

After the sample sweeps, the numbers of mosquitoes biting on an exposed forearm during one minute was counted. Five day running averages showed that the peaks of biting activity fall on the same days as the peaks of flight activity. In contrast, Hocking *et al.*, (1950) found that the peaks of flight activity and biting activity were not synchronized at Churchill, Manitoba.

There are few publications on population fluctuations of mosquitoes. There were three peaks of abundance in the population at Churchill, each formed by a different group of species (Hocking *et al.*, 1950). At Whitehorse, Yukon Territory, there were two peaks each due to a different species, and there were differences in the populations in two successive years (Curtis, 1953).

5.2 Daily Flight Activity

The population graphs give no information on the daily pattern of activity so four surveys each lasting 24 hours, were performed during 1961 and five during 1962 to investigate

this. The sampling location and the procedure were the same as for the evening sample already described. Each sample was taken on the hour starting at 0800 hours one day and ending at 0700 hours the following day. Biting rate, temperature, wind, cloud cover, and the time of sunset and sunrise were recorded.

The pattern of activity was similar in each of these surveys; the differences were attributed to the weather. Mosquitoes in the study area are diurnal and crepuscular, that is, the times of maximum activity are at dawn and dusk with little or no activity at night.

The number of specimens caught in each 24-hour count differed with the date (Section 5.1). Table 13 shows that this number ranges from 34 to 279 mosquitoes, and that the percentage of each species also varied; *A. vexans* did not occur until the late June and July counts. When climatic conditions are favourable outside the forest, certain species migrate out so that their forest population is lowered, and other species which do not migrate will appear to be more numerous. This is an unavoidable artifact, so the conclusions from these counts only refer to the general activity in a forest. The percentages in Table 13 are calculated for the entire 24-hour period ignoring hourly variations. A low percentage does not necessarily mean a species is rare; it may be resting, or flying in another locality.

Since the activity pattern of mosquitoes at ground level has been found to be the same for all the counts, with

TABLE 13

The total Numbers and Percentages of the most abundant species of Aedes Mosquitoes caught during 24-hour counts in the Forest at Ground Level.

Date	Total Numbers	punctor	vexans	riparius	communis	excrucians
1961						
1-2 June	113	33%	0%	12%	30%	3%
23-24 June	62	24	26	18	8	2
6-7 July	84	32	35	4	2	2
25-26 July	163	13	47	1	12	4
1962						
7-8 June	146	21	0	16	35	3
19-20 June	279	30	0	7	13	27
3- 4 July	34	29	24	0	15	18
12-13 July	144	17	33	6	4	17
19-20 July	43	26	16	0	7	21

modifications depending on the weather, the detailed results of only two of them, 1 - 2 June and 25 - 26 July 1961, are presented in Fig. 20.

Both graphs show a rapid rise in activity to a maximum in the evening followed by a drop to almost zero after dark. At sunrise and during the early hours of the morning, there is a rise in activity to a second maximum. During the main daylight hours, 1000 to 1800 hours, activity drops to a minimum depending on the weather and the season.

On 1 - 2 June, the first part of the morning maximum was due to _A. punctor_, but as the hours progressed the activity of this species diminished and _A. communis_ became the dominant species. There were more _A. communis_ than _A. punctor_ during the evening maximum, perhaps because conditions elsewhere were favourable for _A. punctor_ but not for _A. communis_.

Aedes communis had practically disappeared by the 25 - 26 July count; at this time _A. punctor_ and _A. vexans_ were the dominant species. _A. vexans_ is a tolerant species capable of activity over a wide range of temperatures and saturation deficiencies; it was caught in all samples. _A. punctor_ showed a pattern similar to that of 1 - 2 June: a morning and evening maximum separated by a time of little activity.

Weather conditions on the two days under consideration were different; 1 - 2 June was hot with few clouds, 25 - 26 July was cloudy all day with some scattered rainshowers. The June count shows a drop in activity from 1000 hours to 1700 hours, but in the July count the activity remained at almost

Fig. 20. Page 101.

The results of 24-hour counts on 1-2 June 1961 (A), and 25-26 July 1961 (B). Temperature in degrees Fahrenheit is plotted on the left [illegible]issa, and saturation deficiency in mm. of Mercury on the right abscissa. The line under each graph indicates the hours of darkness.

o———o temperature;

●———● saturation deficiency;

▭ number of mosquitoes per sample.

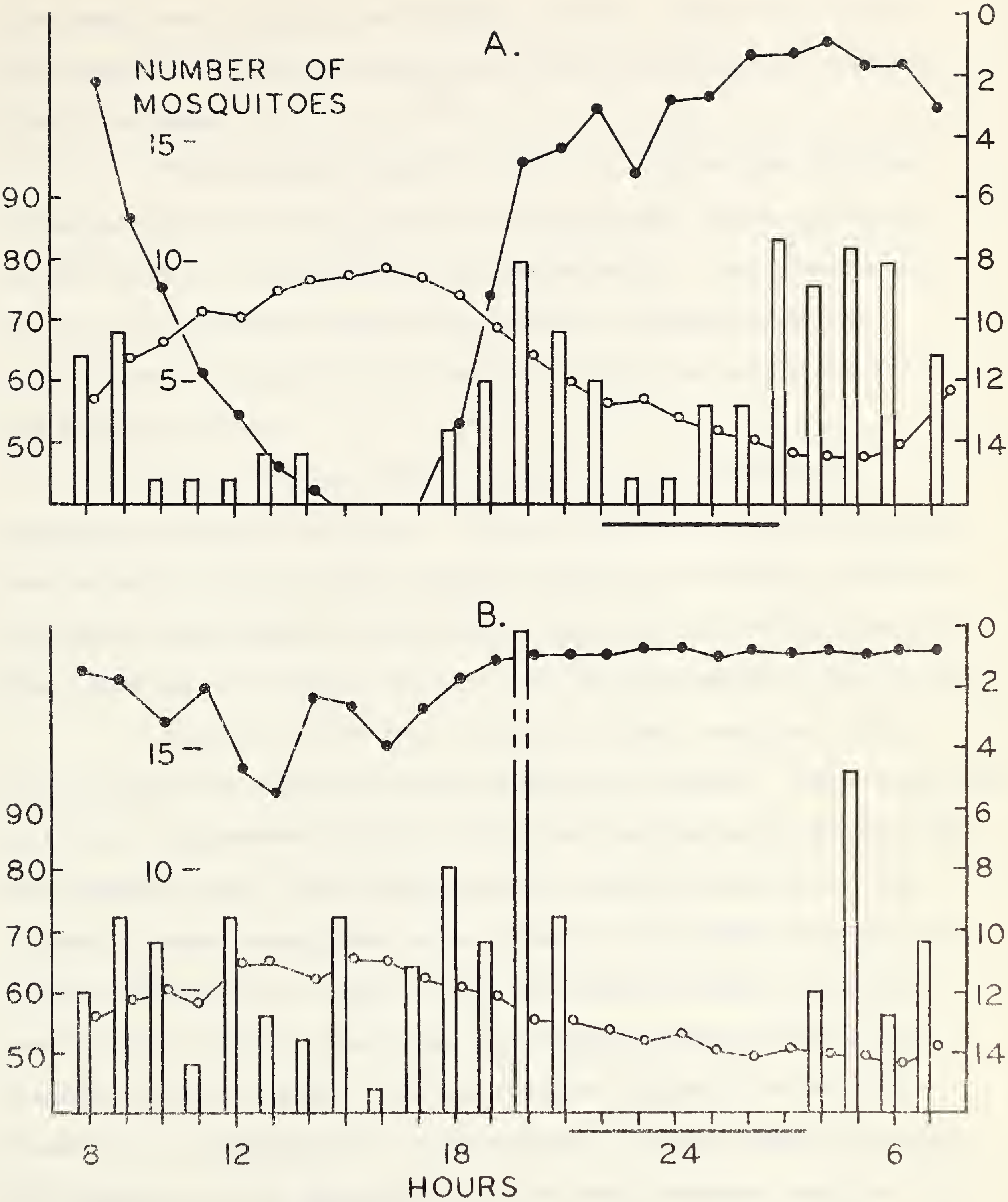

A.
NUMBER OF MOSQUITOES
15
10
5
90
80
70
60
50
0
2
4
6
8
10
12
14
B.
15
10
90
80
70
60
50
0
2
4
6
8
10
12
14
8
12
18
24
6
HOURS

Fig. 20.

the same level during the daylight hours. Since the nights are longer in July, the period of little activity at night is also prolonged.

The activity curves in Fig. 20 follow the changes in saturation deficiency during the daylight hours and there is an inverse relationship with temperature. The cloud cover on 25 July produced relatively constant temperatures and saturation deficiencies, and only a slight variation in the active population.

It is not possible to say that any one factor regulates mosquito activity. These factors are inter-related, and probably all of them regulate activity assuming a greater or lesser importance at different times of the 24-hour period. The importance of these factors will be discussed in Section 6.

During the 24-hour counts in 1961, similar counts were taken five minutes later outside the forest. This sampling site was surrounded by short grass and was about 50 yards from the forest edge. The same procedure was followed as in the forest. Fewer mosquitoes were caught in the open than in the forest (Table 14). Here, as in the forest, there was little activity at night. The times of greatest activity were the same as in the forest, but the species composition was different. *A. communis* was never caught. In the first two counts *A. riparius* and *A. punctor* were the most numerous species. In the last two, *A. vexans* was the dominant species. There were fewer species than in the forest counts showing that only certain species can, or will, migrate out.

TABLE 14

A comparison of the numbers of mosquitoes taken during 24-hour counts in 1961, and the percentage of mosquitoes in the field.

Date	Forest	Field	Percentage in field
1- 2 June	113	19	14%
23-24 June	62	22	26
6- 7 July	84	34	29
25-26 July	163	49	23

During the daylight hours when there is little activity, mosquitoes may be found resting close to the ground on low vegetation in the forest. Flight can be induced if the observer stays in one place for several minutes, or if the vegetation is disturbed. But at night mosquitoes could not be found at ground level, so it was thought that they had either moved up into the higher layers of the forest, or above the forest canopy, or away from the forest altogether.

5.3 Stratification of Mosquitoes in the Forest

To determine whether mosquitoes did move into the higher layers of the forest at night, or at any other time during a 24-hour period, two platforms were built in 1962 (Fig. 21). Two large aspen poplar trees, five feet apart, with straight trunks and no branching except in the canopy layer, were selected for the forest tower. The first platform, 20 feet from the ground, was well above the shrub layer and herbaceous layer of the forest floor, yet below the canopy. The second platform, at 40 feet, was at the beginning of the canopy layer, which then extended for a further ten or fifteen feet to a height of 50 to 55 feet above the ground. The tower was 150 yards from the edge of the forest, and five yards from a path. Since it was only 20 yards from the forest sampling site of 1961, forest samples at all times in 1962 were taken at the tower.

During the five 24-hour counts in 1962, hourly samples and records were taken at three feet, 20 feet, and 40 feet. Since the complete sampling took ten to fifteen minutes there might have been a bias if the stations were always sampled in the same order, a previously decided random order was used.

Climate in the forest

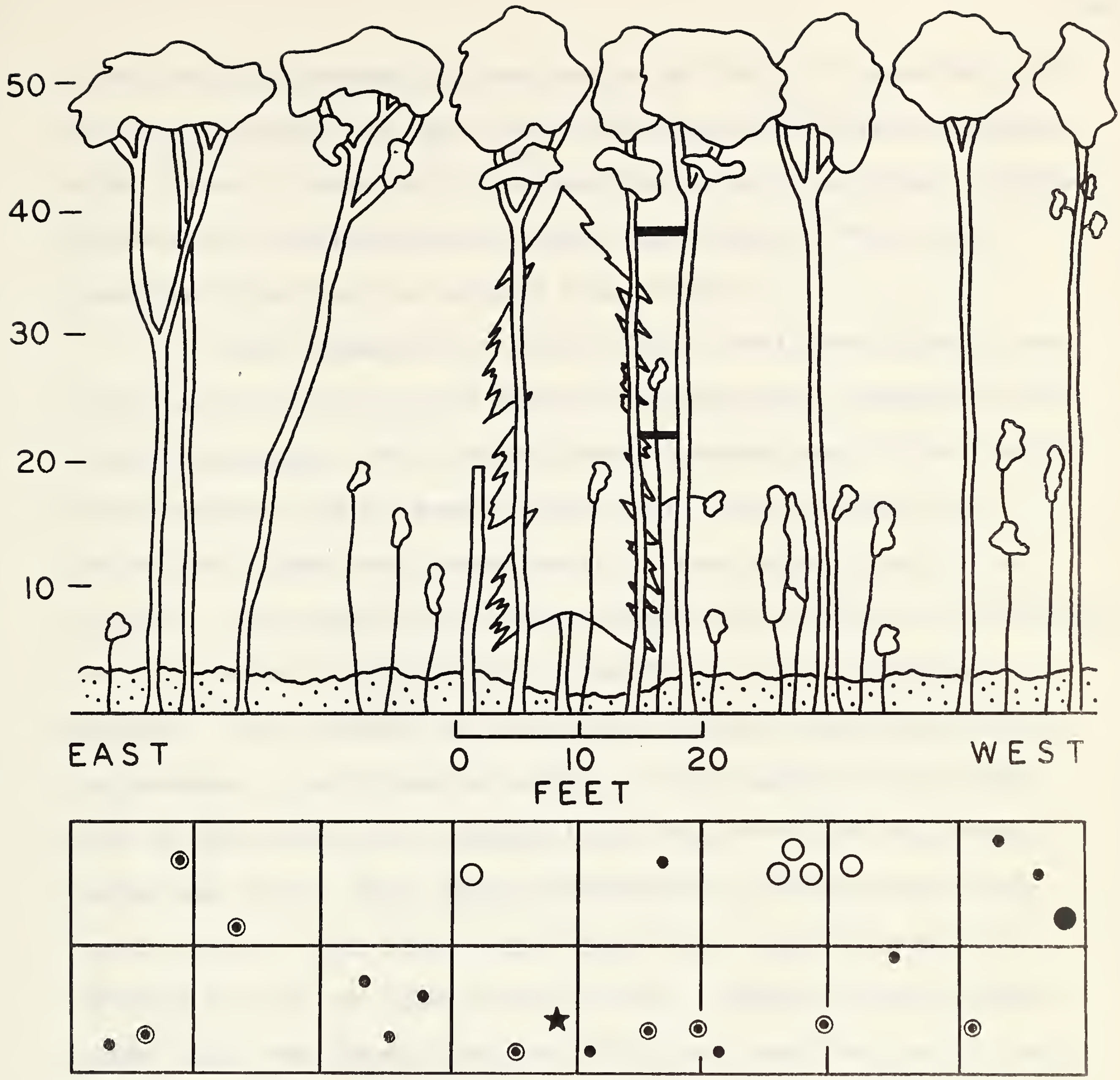
Geiger (1959 - Section 6) has given observations on the daily fluctuations of temperature and relative humidity at various heights in a forest. One example of an old oak

Fig. 21. The tree tower in the aspen forest. The first platform is 20 feet above the ground, the second 40 feet. The bottom of the photograph is about 8 feet above the ground. June, 1962.

stand in Germany, shows that at sunrise there is an inversion of the temperature: it is coldest in the canopy and warmest on the forest floor. As the sun rises, a temperature stratification is reached; the canopy is the warmest region and the temperature decreases above the canopy in the free air, and below it in the trunk space. Haddow and Corbet (1961) have given readings for a forest in Uganda. In this instance, the canopy at 56 feet was generally cooler than the free air above, and the forest floor below. At no time was the canopy the warmest region, not even during the daytime. These authors found that afternoon rain affected the temperature pattern of the day.

Temperature, humidity, and light intensity readings were taken at the three levels at each sampling time. The 'ground layer' readings were taken at the edge of the path three feet above the forest floor, the 'middle layer' readings from the 20 ft. platform, and the 'canopy layer' readings from the 40 ft. platform. 'Free air' readings are those recorded by the thermohygrograph (see Section 1.2) in the open. In the dense herbaceous vegetation growing on the forest floor, it is generally cooler and more humid than at 3 feet above the forest floor. Mosquito flight is limited by the denseness of this vegetation.

The climate was similar at all levels in the mature aspen forest. The profile of the forest (Fig. 22) at the tower shows the three main layers: 1) the herbaceous and shrub layer characterised by thick vegetation, 2) the middle



- ◉ Aspen poplar Populus tremuloides - large
- • Aspen poplar P. tremuloides - small
- ● Balsam poplar Populus balsamifera
- ★ White spruce Picea glauca
- ○ Birch Betula papyrifera

Fig. 22. Profile and plan of the aspen forest at the tree tower, showing ground, middle, and canopy layers. The platforms are on the two central aspen poplars.

layer mainly composed of the trunks of the tall trees and, 3) the canopy where the tall trees form branches densely clothed with leaves. Because of the open nature of the forest, shafts of sunlight can penetrate through the canopy. This has a profound effect on the ground temperature.

The temperature at all three levels was either lower than, or the same as, the free air temperature recorded by the thermohygrograph. The ground layer temperatures in the forest never reached higher temperatures than the free air even during the night when radiation from the ground outside is highest. From about 2300 hours onwards the forest is isothermal, and it remains so until 0700 or 0800 hours the following morning. Even during the afternoon on hot sunny days, little temperature stratification occurs. For example, on 12 June 1962 at 1600 hours the canopy layer was 77°F, and the ground layer was 76°F. This small difference in ground and canopy layers exists even though the temperature range during the 24-hour period was from 49°F to 77°F. Sometimes during daylight hours the canopy may be 2°F higher than the ground layer for an hour or so; later the ground may be warmer than the canopy. At other times, the middle layer may be a degree higher than either canopy or ground layers. Any divergence in temperature during the daytime is soon corrected, so that by 2300 hours all layers are isothermal.

The similarity between the three layers may be attributed to 1) the open nature of the forest, 2) the stratification of the leafy layers, and 3) the low density of the canopy.

Except at night when the air is saturated, there are normally differences between the relative humidities of the ground layer, the middle layer, and the canopy layer. The humidity is highest in the ground layer, and lowest in the canopy. If there is a strong wind, the canopy layer has a considerably lower relative humidity, even at night. However, the canopy layer is always more humid than the free air. The daily range in relative humidity in the aspen forest is similar to that described by Geiger (1959, p. 334): "From its lowest value at the time of the morning temperature minimum when all layers are close to saturation, the difference rises about 5% at daybreak and until midday remains at approximately this point. In the late afternoon, it again begins to increase and reaches a point which is, on the average, between 15 and 20%. From then on the difference decreases steadily until it again reaches its minimum between midnight and sunrise."

These readings show that there is almost as great a range in daily temperature in the three forest layers as there is in the free air. Any differences in temperature in the forest are insufficient to act as a climatic barrier to mosquito movements. There are greater variations during the daytime in the relative humidity readings but even these cannot be classed as barriers. Certain mosquito species have been observed flying in the open when temperatures were higher and relative humidities lower than those in the higher layers of the forest. There thus seems no climatic reason why mosquitoes should not be found in any layer of the forest.

Movements of mosquitoes in the forest

Most of the published information on the stratification of mosquitoes is from tropical forests (e.g. Bates, 1944; Corbet, 1961a; Haddow, 1945a, b, 1954, 1960; Haddow and Highton, 1947; Mattingly 1949; Pittendrigh, 1950a, b). In these studies, the rhythm of activity and the location of the species show much variation; some mosquitoes are entirely diurnal, others are nocturnal; some are found in the canopy layer, others only at lower layers.

Less has been published on this subject in North America. Snow (1955) studied the movements of mosquitoes in cypress, *Taxodium distichum* (L.), forests in Tennessee. Here, too, there are diurnal, crepuscular, and nocturnal species which are active at ground level and in the canopy. Within the forest, Snow (*op. cit.*) observed two general vertical movements: 1) a diurnal movement upwards along the main tree trunks with horizontal spreading in the canopy, and 2) an evening movement upwards into the canopy followed by a descent to ground level at dawn. Of the species in Snow's study only *Aedes vexans* and *Mansonia perturbans* occur at Flatbush. Love and Smith (1958) captured mosquitoes at various heights above the ground with mechanical sweep nets, and plotted the distribution of the genera. *Aedes* was found most abundantly at ground level and from 15 to 40 ft. above the ground. No information is given on habitat, type of country, or times of collection. Burgess and Haufe (1960) used traps with a moving striped pattern to attract mosquitoes at 5, 25, and

50 feet above the ground. Results were obtained from open prairie in southern Alberta, and in a mixed ash and American elm forest in Ontario. For each of the abundant species considered in the prairie sample (*A. dorsalis*, *A. spencerii*, *A. vexans*, *Culiseta inornata*, and *Culex tarsalis*), the total number caught decreased with height. Each species showed a maximum activity at dusk, and for *A. spencerii* at sunrise as well. However, the forest sample showed that 53 per cent of the total number was taken at the 25 foot level, 29 per cent at the 5 foot level, and 18 per cent at the 50 foot level; that is, 71 per cent of the population during a 24-hour period was flying at, or above, the 25 foot level. MacCreary (1941) used light traps at 5 and 100 feet above the ground, and found that the traps at 100 feet caught 3, 8.5, and 5 per cent of the total number of female mosquitoes.

The North American authors cited used equipment able to capture mosquitoes continuously at all hours of the day and night. This was not possible in the present study and the results are based on sample sweeps. The few minutes when each sample was taken may not have been typical of the hour as a whole. On the other hand, this method of sampling is not biased by relying on the visual or auditory responses of the mosquito; any mosquitoes caught were a sample of the population in unorientated flight.

Few mosquitoes were found in the middle and canopy layers of the forest. Altogether 562 mosquitoes were caught in five 24-hour counts; 546 at ground level, 15 at 20 feet and

2 at 40 feet. The 20 and 40 feet samples correspond to 2.8 per cent of the total, a figure much lower than the 71 per cent obtained by Burgess and Haufe (*op. cit.*) under almost comparable conditions. Of the 12 species recorded at ground level, six were found at 20 feet (*A. communis*, *A. excrucians*, *A. intrudens*, *A. punctor*, and *A. riparius*) and two at 40 feet (*A. flavescens* and *A. punctor*). *Mansonia perturbans* and *A. vexans* were also found at 40 feet, and *M. perturbans* and *A. fitchii* at 20 feet (Section 5.5).

Most of the mosquitoes were caught during the crepuscular period. There were few mosquitoes in the higher levels of the forest at night, so it is probable that there is a slight migration upwards at dusk and a descent at dawn, but affecting such a small portion of the population as to be unimportant and unnoticeable. During the times of maximum activity at ground level, it was possible to remain at the higher levels without being bothered by mosquitoes at all. The small percentage that is found at 20 and 40 feet does not suggest that there is a mass migration as has been recorded in other regions and forests of the world.

5.4 Flight Activity of five species of *Aedes*

The evening samples and counts at various levels in the forest showed that the flight activity of the principal species differed. Some species were never found during the main part of the day, others were caught in small numbers.

It is important to distinguish between biting activity and flight activity. Mattingly (1949) thought that biting activity was a measure of flight activity, so that the maxima of both activities would be at the same time. Haddow (1961) showed that this is not so; flight activity may be highest when biting activity is low, and vice versa.

In the present study, the flight activity graphs for each species at ground level were calculated from nine 24-hour counts. The scarcity of mosquitoes at 20 and 40 feet does not allow activity curves to be calculated for these heights. Even at ground level there are only sufficient details for five species: *A. communis*, *A. excrucians*, *A. punctor*, *A. riparius*, and *A. vexans*.

Rapid fluctuations in an insect population are common. Similarly there may be wide variation in samples caught at a particular hour on different days because of past and present weather conditions, and the age of the population. The values used in this analysis are the means of nine samples. Arithmetic means are unsatisfactory since a single high value raises the mean to a disproportionate figure; more satisfactory is a modification of the geometric mean first used by Williams (1937). Haddow (1960) has called this modified geometric mean the Williams' mean (M_W) calculated by the formula:

$$\log (M_W + 1) = \frac{\log (n_1 - n_\infty + 1)}{N}$$

where n_1, n_2, etc. to n_∞ are the individual readings in a

series of N observations. One (1) is added to each reading, to eliminate the effects of zero values, before conversion to logarithms. After summing the logarithm values, one (1) is subtracted from the antilogarithm. This value is the Williams' Mean; it may be plotted as such, or as M_W x 100 or, as in this study, as a percentage of the total M_W readings.

Two examples will clarify the advantages of the Williams' mean. Table 15 shows the number of _A. excrucians_ caught in four series of nine samples. The arithmetic mean is higher for the 1000 hours sample because of one unusually high reading, whereas the Williams' Mean shows that the 1100 hours sample is largest. In the other example, the arithmetic means are the same due to one high reading in the 0600 hours series, but the 0700 hours series has the higher Williams' Mean; the activity at 0700 hours is higher than at 0600 hours.

The five flight activity curves show some similarity; there are peaks of activity in the evening and the early morning. However, there are some important differences between the species.

A. communis has peaks of activity at 2100 and 0600 hours, and another small peak at 1000 hours. There is a rapid fall in activity between 2100 and 2200 hours, although unlike other species some activity occurs at all hours during the night. The rise to maximum activity in the evening is gradual, a contrast to the erratic rise to the morning maximum.

A. excrucians is similar to _A. communis_; the times of maximum flight activity are 2100 and 0700 hours, and there

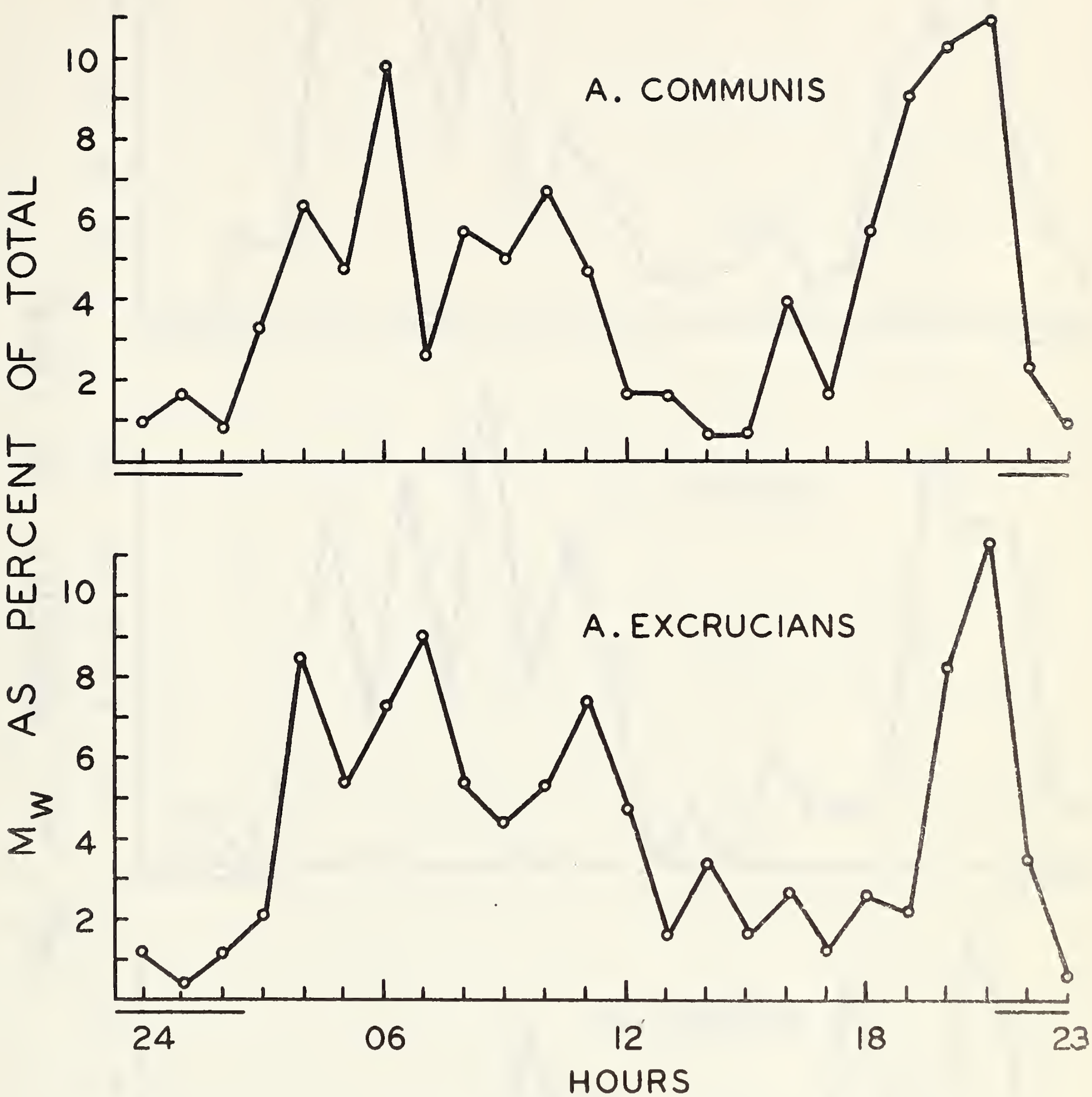


Fig. 23. Flight activity graphs for A. communis, A. excrucians, A. punctor, A. riparius, and A. vexans based on 24-hour counts in 1961 and 1962. The numbers of mosquitoes are plotted as the Williams' mean, expressed as a percentage of all the mosquitoes of the species caught. The line under each graph indicates the hours of darkness.

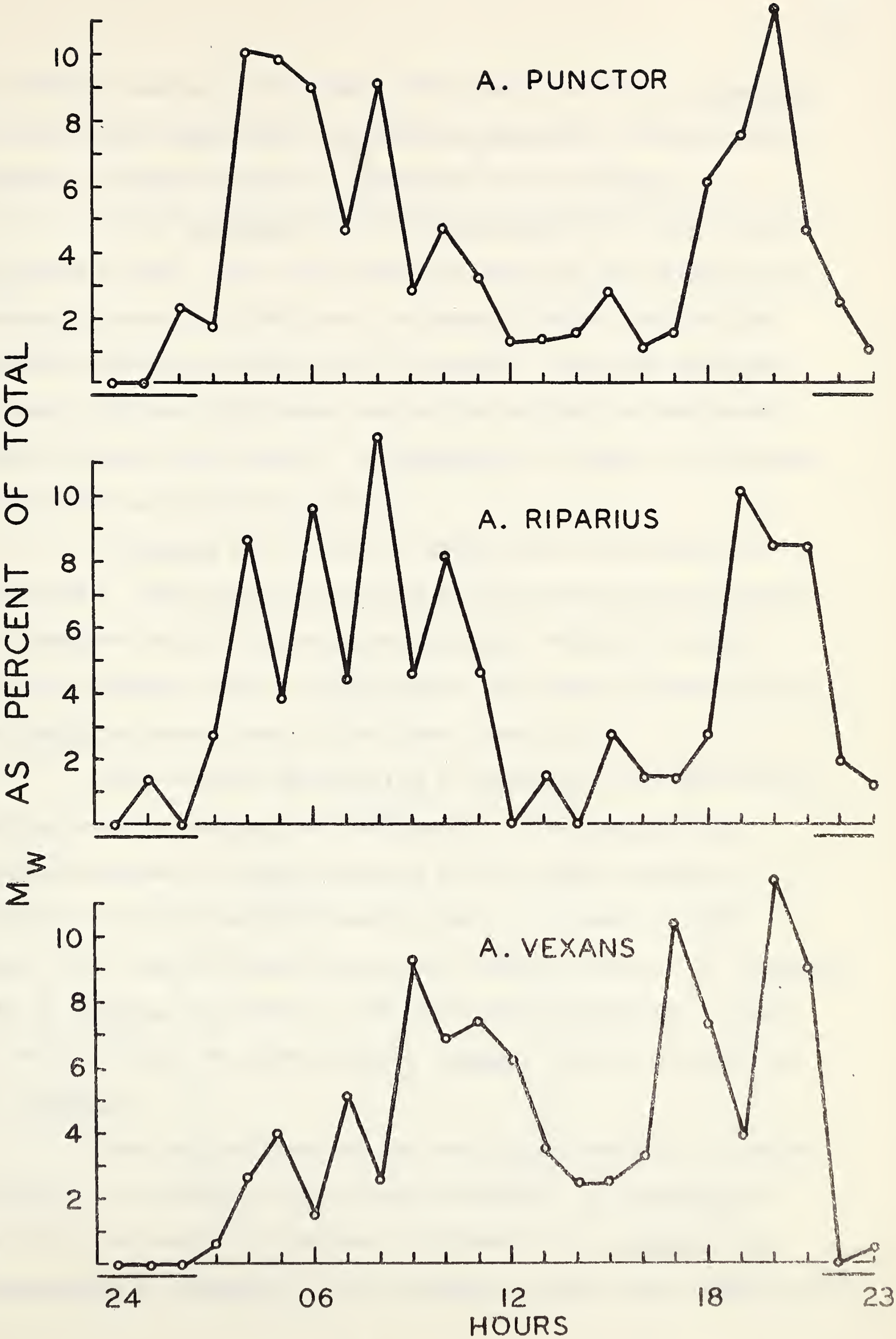


Fig. 23 (continued)

is another peak at 1100 hours. This peak, as for A. communis, is four hours later than the morning maximum. In both these species, flight activity is greatest in the evening.

In A. riparius the morning maximum is higher than the evening one. As in the previous species, the rise to the evening maximum at 1900 hours is gradual while that to the morning maximum at 0800 hours is erratic. The low activity between 1200 and 1700 hours may be due to part of the population leaving the forest. A. riparius is common in the open during the main daylight hours.

A. vexans has a peak at 0900 hours and another at 2000 hours. The activity is high at 1700 hours and yet there is a decline before the evening maximum. There is little activity between 2200 and 0300 hours, but more activity during the daylight hours than in the other species.

The evening maximum for A. punctor is at 2000 hours and the morning maximum at 0400 hours. The rise to the morning maximum is rapid compared to the other species. Activity falls after 0400 hours, rises to a peak at 0800 hours, and then declines during the daylight hours. A. punctor like A. vexans, is found in the open during daylight. There is more activity at night than A. vexans, but not as much as A. communis.

The main difference in the flight activity of these species is the time of the morning maximum. A. punctor is the first to reach its maximum, followed by A. communis, A. excrucians, A. riparius, and A. vexans in this order (Table 16).

TABLE 15

Numbers of A. excrucians captured at four fixed times for nine days.

Time hours	Numbers per sample	Total	Arithmetic Mean	Williams' Mean
0600	0,0,0,2,1,4,0,1,0	8	0.88	0.57
0700	0,1,1,1,1,3,0,1,0	8	0.88	0.71
1000	0,0,0,0,0,10,0,1,0	11	1.22	0.40
1100	0,0,1,0,0,3,0,3,1	8	0.88	0.57

TABLE 16

The main features of the flight activity curves for five species of Aedes.

Species	Time of maximum activity morning	evening	Highest peak	Time of mid morning peak
A. communis	0600	2100	Evening	1000
A. excrucians	0700	2100	Evening	1100
A. punctor	0400	2000	Evening	1000
A. riparius	0800	1900	Morning	1000
A. vexans	0900	2000	Evening	1100

The species which reach their peaks first, do so at a time of rapidly changing light intensity. However, by the time the later species, A. riparius (0800 hours) and A. vexans (0900 hours), reach their peaks, light intensity is almost stable although temperature and humidity readings are still changing. A. riparius and A. vexans reach their evening peaks by 1900 and 2000 hours respectively while the light intensity is still high, but when temperatures are already falling. The evening maximum of A. communis and A. excrucians is at a time of changing light intensity. A. punctor does not fit into this pattern. The activity in all species falls between 2100 and 2200 hours. On the Gulf of Finland (60 - 61°N. lat.), A. communis shows peaks of biting activity at 0300, 1000, and 2200 hours; biting activity is higher at night than during the day (Syrjämäki, 1960).

In summary, all species for which there is sufficient information, have a trimodal flight activity pattern. Activity during the main daylight hours is reduced and there is usually no activity during the hours of darkness.

In temperate regions, even in an aspen forest, environmental 'clues' are clearcut, and consequently only small differences would be expected in the activity curves of the different species if they were controlled only by the environment. Corbet (1960) has pointed out that "poorly-synchronized activities occurring at ground level in a tropical forest are probably positioned mainly by endogenous processes, whereas well synchronized crepuscular behaviour typical of exposed

situations is doubtless controlled exogenously." Since day, night, and twilight are well defined in the study area, it is interesting that the activity curves of the five species are not synchronized. They are partly controlled exogenously but there may be a strong endogenous rhythm, varying from species to species, modifying the response to exogenous stimuli. In some species, activity may be controlled mainly exogenously, while in others the behaviour is due to a combination of endogenous and exogenous rhythms; perhaps this is why the activity curves are different.

5.5 Biting Rates during the Afternoon and at Night

There are many studies on the biting habits of mosquitoes, e.g. Bates (1944), Corbet (1961b), Haddow (1945a, 1954, 1960, 1961), and Kumm and Novis (1938). Several types of biting behaviour are apparent: diurnal with a peak at mid-day, diurnal with peaks at dawn and dusk, and nocturnal with peaks at various times of the night. Each of these types may be modified at different levels in the forest. In the aspen forest, the changes in biting activity during the 24-hour period closely follow the flight activity changes (Section 5.2). Biting rates were recorded in mid afternoon and at night at ground level, 20 feet, and 40 feet so a comparison could be made, and any effects of moonlight could be determined.

Opinions differ on whether moonlight has any effect on the flight of insects. It is well known that light traps

do not catch many insects on moonlit nights, but this may be because the moon competes with the light trap. It does not prove that fewer insects are flying on moonlit nights. Williams and Singh (1951) found that more insects came to their light trap at new moon than at full moon, and they concluded that moonlight had an effect on their catches. In a later paper (Williams, Singh and El Ziady, 1957) they were "without any evidence of an effect of moonlight on the activity of night flying insects ...." Provost (1959) using a light trap showed a lunar periodicity of flight activity with a peak just after new moon, while a non-attractant air sampling device showed no such periodicity. He concluded that there was no evidence for a moon phase effect on the flight activity of mosquitoes, and any periodicity is due to a physical cycle in the attracting efficiency of the trap. However, the moon probably does increase the activity of nocturnal mosquitoes (Corbet, in press). There is evidence that <u>Anopheles</u> (Ribbands, 1946) and <u>Mansonia</u> (Snow and Pickard, 1958) show a cyclical activity depending on the moon phase. I did not use light traps so the only attracting effect was an olfactory one.

In this study, the biting rate was the number of mosquitoes biting on an exposed forearm during a 15 minute period; during the evening samples, exposure was for one minute only. Four sets of observations were made between 1400 and 1500 hours in mid June, and five sets between 2400 and 0100 hours.

In the afternoon, biting rate was highest at ground

TABLE 17

Numbers of mosquitoes biting during 15 minute periods between 1400 and 1500 hours at ground level, 20 feet, and 40 feet.

Date - 1962	Weather	*A. cinereus*	*A. communis*	*A. excrucians*	*A. fitchii*	*A. implicatus*	*A. intrudens*	*A. punctor*	*A. riparius*	Unidentified	Total
Ground level											
7 June	Overcast		14				1	7	5		27
12 June	Mixed		2	1	3	2	1	4	4		17
13 June	Sunny	2	5		3			4	2		16
14 June	Sunny		2		2	1		7	4		16
											76
20 feet											
7 June	Overcast		1				1				2
12 June	Mixed							1			1
13 June	Sunny										0
14 June	Sunny						1			1	2
											5
40 feet											
7 June	Overcast						1			1	2
12 June	Mixed										0
13 June	Sunny										0
14 June	Sunny										0
											2
Totals:		2	24	1	8	3	5	23	15	2	83

TABLE 18

Numbers of mosquitoes biting during 15 minute periods between 2400 and 0100 hours at ground level, 20 feet, and 40 feet.

Date - 1962	Phase of moon	A. canadensis	A. communis	A. excrucians	A. fitchii	A. intrudens	A. punctor	A. riparius	A. vexans	Mansonia perturbans	Total
Ground level											
8 June	None							2			2
20 June	Full		6	7	2		3				18
4 July	None	1					1				2
13 July	3/4			1	1		4	1	7		14
20 July	Full, below horizon			3	1		1			1	6
											42
20 feet											
8 June	None							1			1
20 June	Full		1				3				4
4 July	None									1	1
13 July	3/4						1		1		2
20 July	Full, below horizon				1		1				2
											10
40 feet											
8 June	None					2					2
20 June	Full		1				1				2
4 July	None										0
13 July	3/4								1		1
20 July	Full, below horizon									1	1
											6
Totals:		1	8	11	5	2	15	4	9	3	58

level (Table 17), and the overcast day had a higher biting rate than the less cloudy days. Mosquitoes were also biting at 20 feet and 40 feet. _A_. _communis_, _A_. _intrudens_, and _A_. _punctor_ were the only species biting at the higher levels; the other five species were caught at ground level only. The ratio of the number of mosquitoes biting at ground level to the combined number at 20 and 40 feet is 11:1.

At night the procedure was the same, but the results were very different (Table 18). The biting activity was lower than in the mid-afternoon. _A_. _communis_, _A_. _excrucians_, _A_. _fitchii_, _A_. _punctor_, and on 13 July _A_. _vexans_, were the main species biting at ground level at night. Taking all levels into consideration, _A_. _punctor_ and _A_. _excrucians_ were the most numerous species. _A_. _communis_, _A_. _punctor_, _A_. _vexans_, and _Mansonia perturbans_, a species not found during the daytime, were caught at all three levels. The ratio of the number of mosquitoes biting at ground level to the combined number biting at 20 and 40 feet is 2.6 : 1, i.e., there is less differentiation between levels at night than in the daytime.

There is a difference between the total number of mosquitoes biting on each night. At ground level, few were caught on 8 June, 4 July, and 20 July but more were taken on the nights of 20 June and 13 July. The same trend is evident for the 20 and 40 feet captures. Those nights with a high biting rate were nights with a three-quarter or full moon high in the sky. The nights with low biting rates either had a new moon or no moon at all. The light intensity on a moonlit

night is comparable to that at the end of the evening twilight and the beginning of sunrise. My results indicate that biting activity is nearly five times greater on moonlit nights than on non-moonlit nights.

5.6 Flight and Biting Activity in different Habitats

Observations in 1961 showed that the number of mosquitoes found in willow scrub, immature aspen forest, and open grasslands was not the same as in the mature forest. In 1962, I tried to evaluate this difference.

Five locations were chosen for this study: 1) the mature forest at the same place where the regular sampling was made; 2) a grove of immature aspen; 3) a path in willow scrub surrounded by isolated black spruce trees; 4) the 20 ft. platform in the forest; and 5) an open field 50 yards from the forest edge. Since readings and samples were made between 2000 and 2030 hours, a time of changing light intensity, the locations were visited in a different sequence each time. However, the forest was always sampled first so the seasonal population studies were not affected.

The first series of observations was from 12 - 24 June (no readings for 16 June), and the second series from 13 - 24 July. At each location the flight activity and biting activity were recorded as described in Section 5.1. The geometric mean (Williams' mean) was calculated for each set of 12 day observations for each habitat.

The number of mosquitoes biting (biting activity) cannot be higher than the number flying (flight activity) since a mosquito must fly to its host before it can bite. My data on biting activity and flight activity cannot be compared directly because they are arbitrary numbers based on different sampling methods: biting activity was the number of mosquitoes biting on the forearm in one minute, and flight activity the number of mosquitoes caught in 10 sweeps. The average values for biting activity were often higher than the average values for flight activity. The flight activity and biting activity for the June and July observations are shown in Fig. 24; this Figure also shows the change in the relationship in each habitat, *i.e.* the number of mosquitoes biting compared to the number flying.

In June the flight activity and biting activity are very low at 20 feet in the forest (see also Section 5.5) and in the open field. Excluding these two habitats, flight activity is about equal in the immature forest and the willow habitat, and highest in the mature forest. The biting activity was lowest in the immature forest and highest in the willow. In relation to the number of mosquitoes flying there is a greater chance of being bitten in the willow habitat than in the mature forest.

The July results are similar but all the values are lower. It is fortunate in some ways that there was no second brood of *A. vexans* as in 1961 which would have made a comparison between the months less useful.

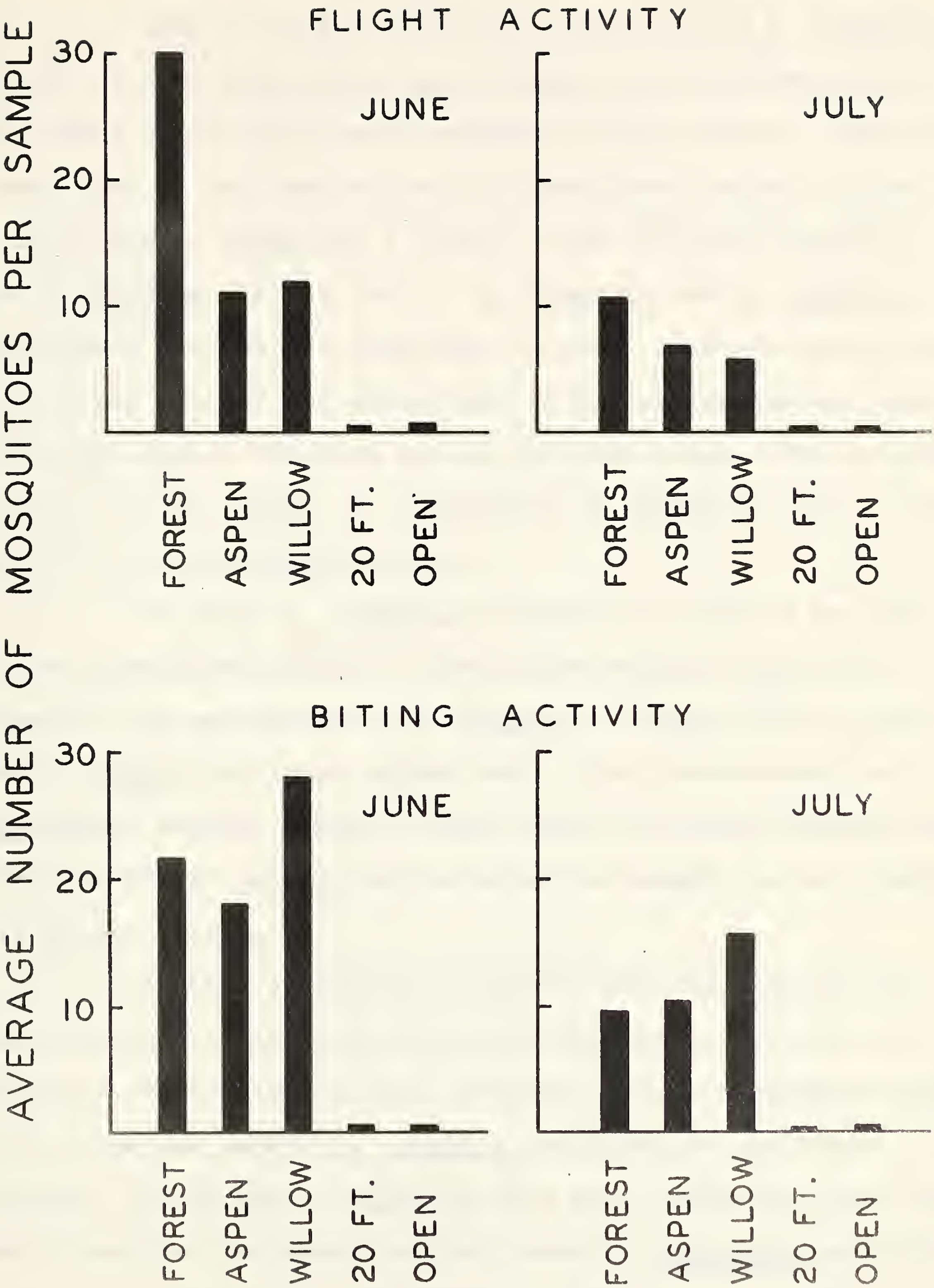


Fig. 24. The average number of mosquitoes in different habitats, June and July, 1962. The flight and biting activity for 12 sets of observations is expressed as Williams' mean.

Table 19 shows that 36 per cent of the A. communis in the 12 - 24 June series were caught in the willow habitat; the other species were most abundant in the forest. Table 20 shows that 24 per cent of the 161 mosquitoes caught in the willow were A. communis, a figure slightly lower than that for A. punctor (26 per cent). A. communis and A. riparius are common species and persistent biters; together they account for 39 per cent of the mosquitoes in the willow habitat, and this may explain the high biting activity there. The principal species in the forest, A. excrucians, A. fitchii, and A. punctor are not such persistent biters.

In July, A. communis accounted for only 4 per cent of the mosquitoes flying in the willow habitat (Table 22). However, the percentage of A. punctor is higher than in June, and A. vexans now forms 24 per cent. The percentages for A. punctor in forest, immature aspen, and willow are similar, as they are for A. vexans, so the relative numbers in each habitat are almost constant.

Another interesting feature from the same set of observations is the distribution of the species between the habitats (Tables 19 and 21). In June, the largest percentage of all species except A. communis was found in the forest. In July, all except A. riparius were most abundant in the forest. Next to the forest habitat, more A. excrucians are found in the immature aspen than elsewhere, and more A. fitchii are found in the willow. Similar percentages of A. punctor are found in aspen and in willow environments; A. vexans also occurs

TABLE 19

The percentage distribution by species of the six principal mosquito species between different habitats. 12 - 24 June, 1962.

Species	Forest	Aspen	Willow	20 ft.	Open	Total Numbers
A. communis	33	31	36	0	0	106
A. excrucians	75	18	7	0	0	88
A. fitchii	67	13	19	1	0	105
A. punctor	62	17	19	0	2	226
A. riparius	48	22	27	0	3	88
A. vexans	0	0	0	0	0	
Other Species	56	18	22	-	4	142
						755

TABLE 20

The percentage composition by species of the mosquito populations of five different habitats. 12 - 24 June, 1962. + = numbers too small for percentages.

	A. communis	*A. excrucians*	*A. fitchii*	*A. punctor*	*A. riparius*	*A. vexans*	Other Species	Total Numbers
Forest:	8	15	16	33	10	0	18	434
Immature aspen:	23	11	10	27	13	0	17	146
Willow:	24	4	12	26	15	0	19	161
20 ft.:	0	0	+	0	0	0	0	1
Open:	0	0	0	+	+	0	+	13
								755

TABLE 21

The percentage distribution by species of the six principal mosquito species between different habitats. 13 - 24 July, 1962.

Species	Forest	Aspen	Willow	20 ft.	Open	Total Numbers
A. communis	63	16	21	0	0	19
A. excrucians	45	37	18	0	0	38
A. fitchii	57	18	25	0	0	28
A. punctor	42	29	29	0	0	122
A. riparius	25	25	45	0	5	20
A. vexans	46	27	24	0	3	86
Other Species	63	16	16	2.5	2.5	32
						345

TABLE 22

The percentage composition by species of the mosquito populations of five different habitats. 13 - 24 July, 1962. + = numbers too small for percentages.

	A. communis	*A. excrucians*	*A. fitchii*	*A. punctor*	*A. riparius*	*A. vexans*	Other Species	Total Numbers
Forest:	7	11	10	32	3	24	13	161
Immature aspen:	3	15	6	39	6	26	5	90
Willow:	4	8	8	40	10	24	5	88
20 ft.:	0	0	0	0	0	0	+	1
Open:	0	0	0	0	+	+	+	5
								345

in equal numbers in both habitats.

5.7 Movement of Mosquitoes into Buildings

On most evenings and nights, female mosquitoes were flying and biting in the wooden hut, 50 yards from the lake, where I lived during this study.

During 1961, *A. intrudens* was the principal species biting indoors. *Anopheles earlei* and a few *Culiseta alaskaensis* were found earlier in the season until the end of May.

In 1962, a sample of mosquitoes landing and biting was taken during the evenings every ten or fourteen days. *Culiseta alaskaensis* and *Anopheles earlei* were the only species from 24 April (when studies began) until 22 May when the first *Aedes intrudens* was caught. From then on, *Culiseta alaskaensis* decreased and none were seen after 27 May. For the remainder of the summer *A. intrudens* and *Anopheles earlei* were the main species. On 23 July, 13 specimens of *Mansonia perturbans* were caught, and on 1 August a single specimen of *Culiseta inornata*. The life history table (Fig. 13) shows how different the *Anopheles earlei* life history was in 1961 and 1962. In 1961, no female *Anopheles* were seen after the end of May, yet in 1962 they were much more numerous and lasted until 23 July. Except for the one specimen of *Culiseta inornata* on 1 August, none of the new generation of female *Anopheles* or *Culiseta* which emerged in July and August were encountered indoors.

For the period 24 April to 1 August 1962, the per-

centages found in the building were: *Aedes intrudens* 48 per cent; *Anopheles earlei* 31 per cent; *Culiseta alaskaensis* 13 per cent; *Mansonia perturbans* 8 per cent; *Culiseta inornata* 1 per cent; and *Culex territans* 1 per cent (total specimens: 164). Thus nearly 80 per cent of all the individuals caught indoors were *Anopheles earlei* or *Aedes intrudens*. None of the abundant *Aedes* species, *e.g.* *A. punctor*, *A. vexans*, *A. riparius*, and *A. excrucians*, were caught indoors although they were caught within a few yards of the building. Many more mosquitoes were found indoors in 1962 than 1961, probably because of the larger population and the extended life span of *Anopheles earlei*.

A. intrudens is classed as a forest mosquito (Carpenter and LaCasse, 1955) but in this study it was rarely caught in the forest. Dyar (quoted by Carpenter and LaCasse, 1955) observed that this species "is fond of entering houses at Banff, Alberta", and Nielsen and Rees (1961) state that it enters buildings to feed. *Anopheles earlei* also has a reputation for entering houses to feed (Rempel, 1953; Pratt, 1953).

5.8 Swarms of Male Mosquitoes

Swarms were rarely observed in the study area; none were seen in 1961, and only 14 in 1962 (Table 23). All were seen in the evening twilight, most of them a few minutes after sunset.

The first swarm, on 22 May, was seen five days after the earliest *Aedes* females (*A. implicatus*) was seen.

This large swarm consisted of *A. implicatus* and *A. punctor*, whereas the other swarms up to and including the one on 5 July were composed of *A. punctor*. Two female *A. intrudens* were caught in the sample from the 17 June swarm. Swarms of male *A. punctor* have been observed by several authors (Frohne and Frohne, 1952; Hocking *et. al.*, 1950; Jenkins and Knight, 1952) in different localities; the sizes of the swarms differed considerably as in the present study.

Three *Anopheles earlei* swarms were observed in September, none at any other time. The individuals in these *Anopheles* swarms showed the erratic flight typical of the females of this species. Nielsen and Haeger (1960) do not give any references to observations of swarming *Anopheles earlei*, although they cite Aitkins' observations of swarms of the closely related *Anopheles freeborni* Aitkin.

No swarms of *A. vexans* were seen although the females of this species were very abundant. In 1961, male *A. vexans* were seen resting on sedge leaves after they had emerged in early July.

Nielsen and Haeger (1960) have classified swarms into four types according to the markers used:

1. 'Top swarms' are formed close to, or above, prominent vertical objects, *e.g.* trees, church steeples, and telephone poles.
2. 'Marker swarms' are formed above a horizontal object contrasting in colour or intensity with its surroundings.
3. 'Free swarms' are formed over a flat surface seemingly

TABLE 23

Records of swarms of male mosquitoes, 1962.

Date	Time hrs.	Time of sunset hrs.	Place	Type of swarm (see text)	Height above ground ft.	Number in swarm	Species
22 May	1930	2038	in path in woods	4	10-15	100's	A. implicatus A. punctor
1 June	2130	2051	above car in open	2	6- 8	40	A. punctor
7 June	2005	2058	at side of tree in forest	1	20-30	50	sight only
7 June	2100	2058	in field, 50 yards from lake shore	3	5-10	200-300	A. punctor
10 June	2010	2101	at side of tree in forest	1	25-30	40	sight only
13 June	2030	2103	on path by side of field	3	6-10	50-100	sight only
17 June	2145	2105	at edge of hut	2	8-10	50	A. punctor
29 June	2145	2107	above car in open	2	6- 8	100	A. punctor
5 July	2145	2104	above car in open	2	6- 8	100	A. punctor
10 Sept.	1930	1904	above Stevenson screen in open	2	10	50	Anopheles earlei
14 Sept.	1900	1845	above Stevenson screen in open	2	10	30	A. earlei
14 Sept.	1900	1845	in field in open	3	10	30	A. earlei

independant of swarm markers.

4. 'Ceiling swarms' are formed when large numbers of males are present covering a large area like a ceiling.

A. punctor formed all four types of swarms while *A. implicatus* was only found in the ceiling swarm on 22 May. *Anopheles earlei* formed free swarms and marker swarms. Top swarms are the commonest type for the subgenus *Ochlerotatus* Nielsen and Haeger, *op. cit.*) which includes all the *Aedes* species, except *A. cinereus* and *A. vexans*, in the study area; in this subgenus, ceiling swarms have been recorded previously for only *A. cantans* (Meigen) and *A. taeniorhynchus* (Wiedemann).

Mating was not observed in any of the swarms.

6. FACTORS REGULATING FLIGHT ACTIVITY

6.1 Introduction and Review

Many environmental factors have been held responsible for determining the times of mosquito activity. Temperature, relative humidity, saturation deficiency, light intensity, and wind have been described as controlling factors although opinions differ on the importance of these factors, *e.g.* Dabrowska, 1959; Haddow, 1954; Hocking *et al.*, 1950; Platt *et al.*, 1958; Rudolfs, 1923; Snow and Pickard, 1957.

Temperature

Rudolfs (1923) found that activity increases with increase of temperature until a lethal limit is reached, but decreases rapidly below 60°F and stops almost entirely below 50°F. He found that the range of temperatures between 68° and 77°F has the greatest accelerating influence on the rate of activity. Mellanby (1940) found that 50°F was the flight threshold for *A. punctor* in Lapland (69° N lat.), and in the Yukon (61°N lat.) Curtis (1953) found that activity ceased below 36°F and was negligible below 40°F. At Churchill, Manitoba (59°N lat.), there did not appear to be any variation in attack between 50° and 80°F (Hocking *et al.*, 1950). Platt *et al.*, (1957) found that *Anopheles quadrimaculatus* Say was active over a wide range of temperatures especially between 20° and 30°C (68 - 86°F). The temperature of the water where a larva was reared might be important as a conditioning factor. It would be interesting to know if adult mosquitoes which had

a prolonged development in cold waters were more active at lower temperatures, than those adults which had developed in warmer conditions.

Relative Humidity and Saturation Deficiency

The moisture in the air can be expressed as relative humidity, or the dryness of the air can be expressed as saturation deficiency. Saturation deficiency is related to temperature and this method of expression is more pertinent when discussing mosquito flight activity. It is the amount of water that a mosquito is likely to lose as a result of the drying conditions of the air which is important, rather than the relative humidity at any given temperature. Haddow (1945a) has shown a positive correlation between activity of *Anopheles gambiae* and relative humidity. Dabrowska (1959) also considers that the 24-hour activity cycle is regulated by the relative humidity. *Anopheles quadrimaculatus* showed greatest activity between 70 and 80 per cent relative humidity at different temperatures (Platt *et al.*, 1957), and Platt, Love, and Williams (1958) have claimed "a 100 per cent positive correlation in nature between relative humidity and the abundance of *Aedes vexans* through the night regardless of elevation, time of night or habitat." This statement is a direct contradiction to my findings. Rudolfs (1923) found that the number of mosquitoes alighting increases in almost linear fashion with increase of relative humidity up to 85 per cent; from 85 to 95 per cent the numbers alighting remained nearly constant.

By contrast, Curtis (1953) found no evidence that saturation deficiency affects mosquito activity, but he did not offer an alternative explanation for changes in activity; during darkness "the limiting factor appeared to be temperature."

Activity in a 24-hour period generally follows the saturation deficiency curve (Fig. 20), but it is clear that sometimes other factors are more important.

Light Intensity

Cloud cover can be included under this heading since the extent of cloud reduces the light intensity. Haddow (1954) says: "With reference to possible release mechanisms, the most important microclimatic factor must certainly be light. Thus a large number of species cease biting at sunset, while others begin to bite at this time, and much the same is true of sunrise. The speed at which many of these changes occur is such that it can be attributed only to the rapid light changes of these periods in the tropics." Present evidence suggests this is true for temperate regions as well.

Hocking *et al*. (1950) found a correlation between activity and cloud cover for tundra species of mosquitoes, but not for forest species. Matheson (1944) suggests that the northern species of *Aedes* are diurnal which implies that light is a regulating factor. In Tennessee, the vertical and horizontal movements of *Mansonia perturbans* were correlated with dawn and dusk changes in light intensity (Snow and Pickard, 1957). Platt *et al*. (1957) state that "light intensity

is the only microclimatic condition which can be correlated with egress from, and ingress to, resting places" by *Anopheles quadrimaculatus*.

Haufe (1961, 1962) studied the responses and adaptations of *Aedes aegypti* (L.) to graded light stimuli. After emergence, sensitivity to light increased with starvation so that before death spontaneous activity occurred in darkness. Thus the light intensity necessary to stimulate flight depends on the hunger state of the individual. The threshold of intensity depends on 'time x intensity', and the rate of adaptation of the eye to light. These facts may explain why there are variations in the typical diurnal pattern of field populations. Therefore, most authors suggest that light intensity plays some part in regulating activity cycles. Whether light is favourable or unfavourable for flight or biting activity depends on the species.

Wind

Wind is antagonistic to mosquito flight. Most authors agree that orientated flight is not possible at wind speeds of more than 12 m.p.h. (Hocking, 1953; Hocking, *et al.*, 1950; Rudolfs, 1923). Klassen (1959) suggests that little spontaneous activity occurs in windspeeds above 12 m.p.h., but that strong winds are important for mosquito dispersal. If there is no wind, airborne scents from a potential host cannot reach the mosquito and so one of the stimuli for flight is lacking. It is probable that windspeed influences the mosquito mechanically

(Hocking et al., 1950). Even in a small area wind speeds vary greatly with the vegetation. There may be a negligible wind inside the forest while outside the wind is strong enough to prevent flight.

6.2 Analysis of 24-hour counts

Analysis of the 24-hour counts in 1962 clarifies some of the factors regulating mosquito flight. If the relative humidity readings for the five 24-hour counts are plotted against the number of mosquitoes caught at each humidity reading, no correlation is seen. Any relative humidity reading may have zero, or ten, or twenty, or forty mosquitoes per sample. More mosquitoes are likely at high relative humidity readings than at low ones but small samples are caught at all humidity readings.

The same is true for temperature. Fewer mosquitoes are caught at high and low temperatures than at median ones (55° - 65°F), but the range of the numbers of mosquitoes caught at a particular temperature is large and variable. Relative humidity and temperature are related so that when one rises, the other falls; for any temperature or humidity reading taken alone, there is no measure of the other variable.

If the numbers of mosquitoes from the 1962 24-hour counts are plotted against saturation deficiency, however, larger numbers are recorded from zero to 2.0 mm. of mercury than from 2.0 to 9.0 mm. of ercury (Fig. 25). The effect of

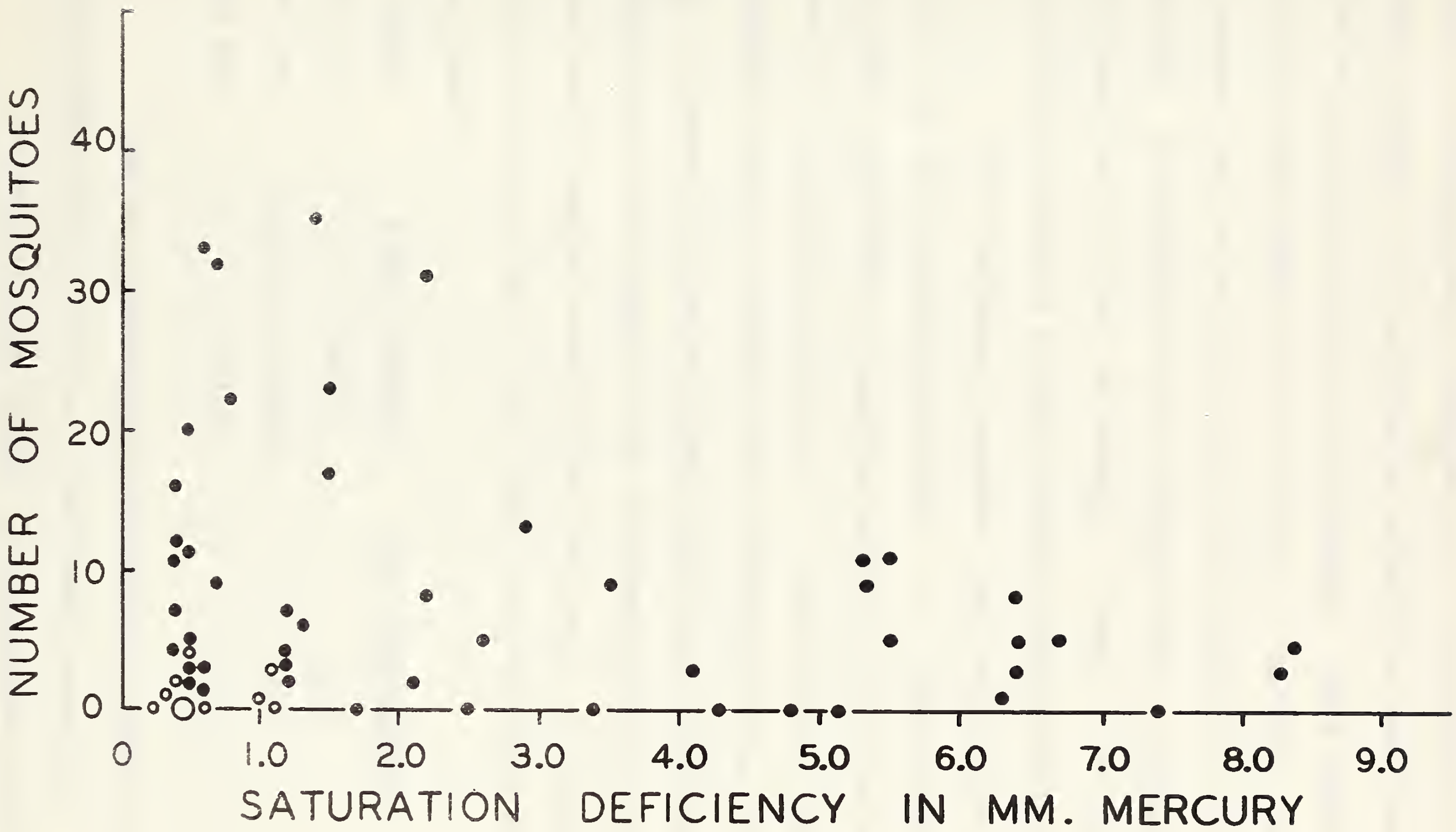


Fig. 25. The numbers of mosquitoes caught at different saturation deficiency readings during 24-hour counts in 1962; ● daytime samples; ○ samples at zero light intensity. The large circle (○) at 0.5 mm. of Mercury indicates ten readings of zero mosquitoes.

saturation deficiency is seen more clearly (Fig. 26) if the number of mosquitoes, expressed as a percentage of the total number caught, at a particular saturation deficiency is plotted against saturation deficiency. More mosquitoes are active in the range zero to 0.9 mm. of Mercury, and there is a gradual fall to no activity in the range 9.0 to 9.9 mm. of Mercury. No mosquitoes were caught above a saturation deficiency of 10.4 mm. of Mercury. There is an inverse relationship between flight activity and saturation deficiency.

Other evidence suggests that saturation deficiency is not the only regulating factor. 1) The 24-hour counts show that the times of maximum activity coincide with the times of low light intensity. 2) Although the times of greatest activity are when the saturation deficiency is low, Fig. 25 shows that under these conditions some small mosquito samples and some samples with no mosquitoes were taken; all these small samples were during the hours of darkness. 3) After a rainstorm on 12 July 1962, the following observations were made:

Time	Light reading	Sat. Deficiency	Sample
2000 hrs.	13 ft. candles	0.55	10
2100 hrs.	6.5 ft. candles	0.55	20
2200 hrs.	0 ft. candles	0.55	0

The only measured environmental factor that changed during these three hours was the light intensity.

If the average number of mosquitoes caught during the 1962 24-hour counts at each light intensity is plotted

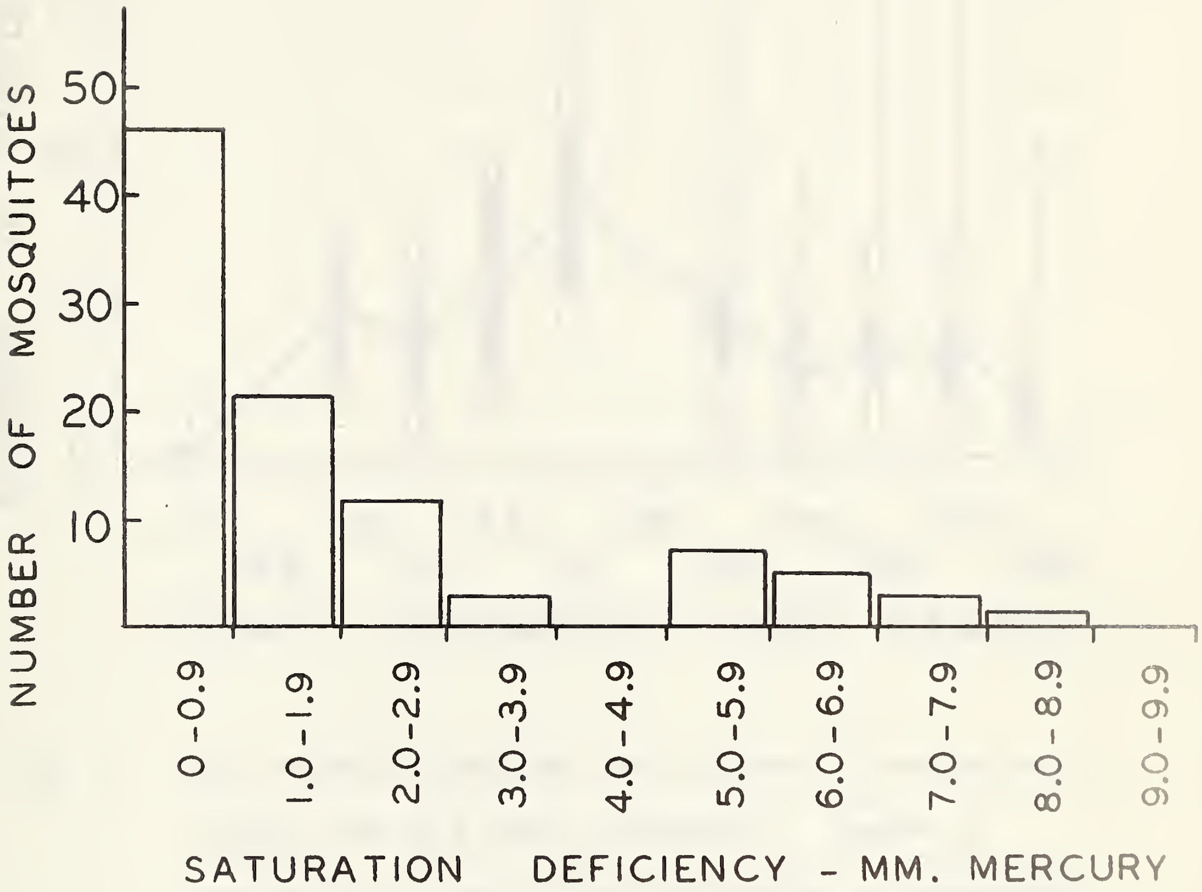


Fig. 26. The relation between the number of mosquitoes in a sample and saturation deficiency in 1962, based on 24-hour counts. The numbers of mosquitoes are plotted as a percentage of all mosquitoes caught.

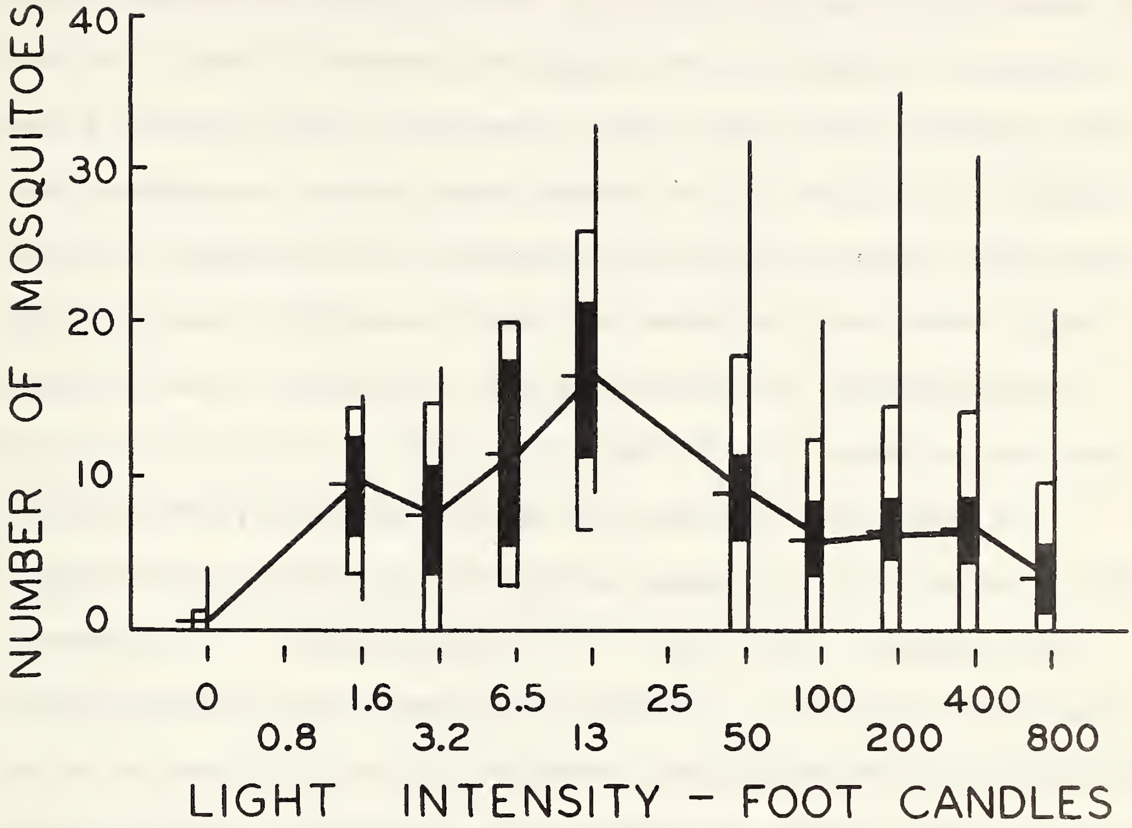


Fig. 27. The relation between the number of mosquitoes flying and the light intensity. Range of variation at each light intensity is expressed by the long vertical line; the mean by the short horizontal line. The blackened part of each bar represents one standard error of the mean on either side of M. One half of each blackened bar plus the white bar at either end represent one standard deviation on either side of the mean.

against the light intensity, the greatest activity occurs at an intensity of 6.5 and 13 ft. candles (Fig. 27). An analysis of variance shows that there is a significant difference (5 per cent level) between the means at each light intensity, and a Duncan's Multiple Range Test shows that although the mean numbers of mosquitoes caught at 6.5 and 13 ft. candles are not significantly different from one another, they are significantly different from the means at the other light intensities. Similarly, the mean numbers of mosquitoes caught at zero, 100, 200, 400, and 800 ft. candles are not significantly different from one another, but they are significantly different from the means at the remaining light intensities. Intensities of 6.5 and 13 ft. candles only occur before sunset and after sunrise. At these times mosquito activity is at its highest, and these results show that the activity is significantly higher at these light intensities than at any other time of the 24-hour period.

Saturation deficiency and light intensity are the two most important environmental factors determining flight activity. Their effects are not independent; it is the combined effect which is the deciding factor. A combination of 13 ft. candles light intensity and a saturation deficiency of 0.5 mm. Hg is most favourable for flight. The number of mosquitoes flying at ideal saturation deficiency readings may be low simply because light intensity is not favourable (e.g. at night).

Saturation deficiency and light intensity each assume greater importance at certain times of day. Dyson-Hudson (1956)

has shown that the activity of *Drosophila subobscura* and *D. obscura* in England is determined by light intensity during the summer months (when temperature is not limiting), and by temperature in the early spring and late autumn when light has only a subsidiary effect. In the present study, saturation deficiency determines the flight activity during the daytime unless the light intensity is above 800 foot candles. At twilight and during the night, saturation deficiency is not limiting and activity is determined by the light intensity. There is a peak of activity at intensities of 6.5 to 25 foot candles, and negligible activity at zero intensity.

6.3 Other factors affecting flight

Wind also affects mosquito activity. In the forests, wind was either absent or very low, and usually not limiting. Several times during the summers, heavy storms swept through the forests; although light intensity and saturation deficiency were favourable, the wind prevented activity. In the open during the daytime, the combination of unfavourable light intensity, saturation deficiency, and wind is not conducive to flight. *A. riparius* and *A. vexans*, for example, fly in the open when conditions are 'unfavourable' for other species.

Observations suggest that most mosquito species stay where the vegetation is dense. Mosquitoes are rarely found in the open or in the upper layers of the forest; most of the time they remain near to vegetation. This is believed to be because

of the climatic conditions associated with vegetation, and it may be a behavioural feature of the mosquitoes in this environment. Species differences are important and so are the factors, other than environmental ones, which initiate flight, e.g., scent and movement. Apparently unorientated flight is mainly limited to forests and willow vegetation.

Haddow (1954) has written: "During the early stages of the investigation the writer inclined to the view that much of the biting behaviour of mosquitoes might be explained in terms of a response to a given set of microclimatic conditions ..... During subsequent work, the view that a mosquito is actively conditioned to bite by a suitable microclimate was gradually abandoned. In its place, the view has developed that a mosquito may be restrained from biting by unfavourable microclimatic conditions or unfavourable local weather and that on removal of the unfavourable factors, it may be 'released' to bite." In my study, the importance of microclimate was also discarded because of the evidence presented earlier.

When climatic conditions are unfavourable for flight, mosquitoes rest in, and under, different types of vegetation. Observations were made during the daytime in 1961 to determine the climatic differences in various types of vegetation, for example in willow scrub, under prickly rose and hazelnut bushes, and in lucerne fields. In the early afternoon of 16 June, the temperature varied from 77° to 82°F, and the relative humidity from 36 to 59 per cent depending on the type of

vegetation. Mosquitoes were found in most places where there was no direct sunlight, especially where there was a dense leafy cover. Although the vegetation showed a range of microclimatic conditions, it appeared although I have no numerical evidence, that the denser the vegetation the more numerous the resting mosquitoes. Mosquitoes were rarely encountered resting in willow groves and immature aspen forests. It might be said that the mosquito makes 'the best out of a bad job' until climatic conditions change. It was not possible to measure the microclimate close to leaf and stem surfaces; it is known that relative humidity decreases rapidly within a few centimetres of a transpiring surface, so the mosquito may be resting in a more favourable environment than indicated above.

Mosquitoes are attracted by the scent of animals, temperature, moisture, movement, contrast, and carbon dioxide (Rahm, 1956), and these factors can stimulate flight and biting reactions over a variety of climatic conditions. Scent is particularly important (Rahm, 1957; Kalmus and Hocking, 1960) whether there is a wind or not. Odour had to be minimised as far as possible in the population studies to avoid erroneous samples. According to Shemanchuk (1958) and Kalmus and Hocking (1960), mosquitoes gradually disperse after a few minutes if the observer keeps still. This is not true in the forests; on arrival in an immature aspen forest on 21 July 1961 (to give just one example), a sample sweep caught three mosquitoes; a similar sweep five minutes later caught 44 mosquitoes.

Mosquitoes react to movement and they will follow an observer far from where they were first attracted, especially from a forest into the open. Consequently a sample from an open habitat must be collected before a sample from a forest. A group of following mosquitoes can be evaded by walking through a building (see Section 5.7) or by running through dense vegetation for 20 or 30 yards. However, mosquitoes do not follow an observer upwards into the middle layer of the forest. If I allowed mosquitoes to accumulate round me at the base of the ladder leading to the 20 ft. platform, they would follow to six or ten feet, the height of the shrub layer, but no further. This was tried many times with the same result.

This, and the fact that few mosquitoes were found in the higher regions of the forest although there was no climatic barrier preventing their movement, suggests that some other factor is involved. Love and Smith (1958) have suggested that the height a mosquito flies at may be influenced by the location of the host. This is true in tropical forests where arboreal animals, for example monkeys, are known hosts. If there is no stimulus, as opposed to no 'barrier', orientated flight will not occur high in the forest. The wind movements in a forest above the shrub layer are mainly horizontal to the ground, so a stimulus originating 20 feet above the ground may never reach mosquitoes at ground level. Hence there will be no movement upwards. If a scent is directed downwards from 20 ft., an unnatural condition, mosquitoes fly up to the scent. This was demonstrated in 1962 using a propeller which

directed a wind of 2 m.p.h. over the observer standing 20 feet up in the forest, down to the ground. After two minutes mosquitoes were flying upwards in the path of the wind, eventually reaching the 20 foot platform. Greater success was obtained in the evenings than during the daytime; for example, 20 mosquitoes landed on me during a ten minute period when the wind was directed towards the ground (*A. cinereus* 8; *A. punctor* 8; *A. fitchii* 2; *A. vexans* 1; *Mansonia perturbans* 1). A ten minute control period beforehand yielded no mosquitoes. The evidence suggests that mosquitoes can, and will, fly in the higher levels of the forest, although under natural conditions the necessary stimuli to take them there are lacking.

7. DISCUSSION

This study was confined to a small area in Alberta, but similar results could be expected in most of the southern boreal forest of Alberta, Saskatchewan, and Manitoba. Further south in the parkland, for example near Edmonton, the mosquito fauna is different.

The histograms of larval abundance show the average number of larvae in each sample for different dates. Certain species are found in particular habitats, and it is interesting that *Wyeomyia smithii* (Coquillett) has not been recorded from Alberta, or Saskatchewan (Rempel, 1953). This species breeds only in the leaves of the pitcher plant, *Sarracenia purpurea* L., and it is this niche which attracts the females. The pitcher plant is found in Saskatchewan (Rempel, 1953), and in northeast Alberta and north of Edson, Alberta (Moss, 1959). It probably also occurs in the marshy areas of the boreal forest of Alberta, but I did not find it in the study area. This is the most specific mosquito - plant association known for these latitudes, and it illustrates best the importance of the plants and the situation of the habitat for the breeding and distribution of a species. The same principle is shown by many species in this study though the differences between the habitats are smaller.

Few adults were seen near the breeding pools; after emergence they migrate from the pools to their preferred environment, most of them to the aspen forests. Once in 1961, male and female *A. vexans* were seen after emergence on sedge

leaves; and in 1962, male and female *A. cinereus* were flying among the vegetation of a grass marsh after emerging. Those species which commonly breed in grass marshes, *e.g.*, *A. cinereus*, *A. excrucians*, *A. riparius*, *A. spencerii*, and *A. vexans* were often found flying in the open. The other species which breed in more sheltered places, except *A. punctor*, are generally confined to the forests and willow scrub, and are not found in the open. *A. intrudens* breeds in grass and semipermanent habitats, and *Anopheles earlei* breeds in permanent waters, yet these species are found almost exclusively in buildings, not near the breeding habitats, or in the open, or in the forests. After emergence, female mosquitoes migrate to a particular environment where they remain for most of their lives.

Presumably only a few mosquitoes of each species secure a blood meal and migrate back to their breeding habitats to lay eggs. The female is induced to lay by the nature of the vegetation, the amount of shade, and the position of the habitat. Vegetation and situation are more important determiners of the species in a habitat than the nature of the water.

Different proportions of the population of a species are found in different environments, *i.e.* they are not randomly distributed; this distribution changes with time. *A. communis* is common in the willow habitat where it breeds, suggesting that this species does not migrate far. The species in the forest come from sedge, grass, and semipermanent habitats, so

they may travel some distance. The flight and biting activity varies in the different habitats as follows:

1. Biting activity is highest in the willow habitat.
2. Flight activity is highest in the mature forest.
3. Flight activity and biting activity are very low in the open and at 20 feet in the forest.
4. The highest biting activity in relation to the flight activity is in willow and immature aspen habitats.

Once female mosquitoes have reached the forest, they tend to remain there unless the climatic conditions outside the forest are favourable. They may then fly outside especially in pursuit of a potential host. There are behavioural differences between the species; some never, or very rarely, leave the forest. In the forest, activity is confined to the lower layers and mosquitoes seldom migrate upwards, probably because no natural stimuli from the higher levels reach the ground. However, mosquitoes will fly upwards if a scent stimulus is directed downwards from the higher levels.

In contrast, male mosquitoes were generally observed in the open, or in the higher layers of the forest. They were mostly seen in swarms, and occasionally elsewhere as single individuals. Few male mosquitoes were caught during the regular evening or 24-hour sampling, so their times and places of activity are different from those of females. All except four of the specimens caught in the forest and willow environments were females of *Aedes*.

Aedes mosquitoes emerge in late May and early June, and most species live until August. The evening samples were collected with the object of following the changes in the population, and it was assumed that the flight activity bears a constant relation to the total population. However, the number of mosquitoes in a sample is also regulated by the climatic conditions preceding the sampling time, so that the numbers caught may be affected by the weather prior to 2000 hours as well as by the size of the population. The fluctuations shown by the flight activity curves cannot be explained on the assumption that all the peaks are real population changes. The maximum number of mosquitoes must occur just after all the *Aedes* have emerged; there is no further emergence to increase or stabilize the population (cf the second brood of *A. vexans* in 1961). Consequently a peak at any time after, say, the middle of June must be due to mosquitoes which were not active previously, and not to mosquitoes which have just emerged. Statistical analysis of the data yielding these peaks shows that in fact more mosquitoes fly in the evening after a hot sunny day than after a cloudy day.

Prediction of the size of the *Aedes* mosquito population is difficult. The total population, and the populations of certain species, differed in 1961 and 1962. The actual population numbers are not known, but the relative numbers each year are determined by:

1. The number of eggs available for hatching.
2. The mortality of larvae and pupae before emergence.
3. The snowfall during the previous winter.

The number of eggs that hatch in the spring is partly dependent on the extent of the pools. If pools are widespread, more eggs will be wetted and immersed, and a larger adult population will follow. After several years of small snowfall (and small pools), there may be accumulations of eggs in regions which were not flooded in these years; a heavy snowfall will then result in a large population the following summer. Whatever the snow conditions it is unlikely that the population is limited by the number of eggs. The combination of a large snowfall in the winter of 1961-62, below average temperatures, and above average rainfall, resulted in a large mosquito population. In the winter of 1960-61, there was a small snowfall, and the following summer had above average temperatures and normal rainfall; the mosquito population was about half that of 1962. The amount of snowfall in the preceding winter is the most important single factor regulating the initial size of the mosquito population.

In 1962, the adult mosquito population was double that of 1961 yet the samples of larvae were only half as large as in 1961. These facts can be reconciled by comparing the water volume, which is related to the snowfall of the previous winter, in the habitats in the two years. There was nearly three times as much snow in the winter of 1961-62, and in early May there was a further twelve inches of wet snow. The water was six inches deep in many locations in May 1961, but 20 inches deep in May 1962, so the water volume was at least four times as great in May 1962 as in May 1961. The discrep-

ancy between the adult and larval population samples can be explained by the larger water volume, and the greater dispersion of _Aedes_ larvae, in 1962.

Predation is not likely to be a controlling factor except when fish are present, or when the habitat is small, or when the pool has nearly dried up. Parasites may control larval populations (Barr, 1958; Laird, 1956), but the importance of parasitism here is unknown.

The date when _Aedes_ emerge depends on the date when the snow melts, and the cumulative temperatures of the snow melt water; the life span of the adult population depends on the natural life span of the species, on the weather during the summer, and the dates of frosts in late summer. Adult females of _Aedes implicatus_ live for about a month, of _A. vexans_ for about two months, of _A. punctor_ for about three months, and of the _Anopheles_, _Culex_, and _Culiseta_ species for about nine months. In 1962 emergence was a week earlier than in 1961 becuase of the earlier snow melt and higher water temperatures. The effect of weather is best shown by _Anopheles earlei_ which overwinters as an adult from the previous year. In 1961, a year of high temperatures, none was seen after May; in 1962 when temperatures were lower and there was more rain, females were found in July. Early frosts in August can kill many _Aedes_ before the life span has been completed.

During the summer, the following factors influence the activity of adult mosquitoes:

1. Saturation Deficiency.

2. Light intensity.

3. Previous environmental conditions.

4. Location.

5. Endogenous rhythm and physiological condition.

The importance of each factor varies during the 24-hour period and during the summer. The effect of any combination of factors depends on the species and the size of the population.

Some species are abundant and others are rare. The species abundant in the study area are those with unspecific breeding habitats; there are more places where they will develop. Also, each species has a 'preferred' environment; there are prairie species, forest species, and tundra species. The study area, although mainly forest, has open 'prairie like' regions. The species common on the prairies, _A. flavescens_ and _A. spencerii_, are rare, but it is probable that if the forests were cut down they would become more numerous. _Aedes dorsalis_ (Meigen), another prairie species, has not been recorded, and typical tundra species, e.g. _A. nigripes_ (Zetterstedt) and _A. hexodontus_ Dyar, do not occur so far south. The percentage of each species in the total population remained almost the same each year; a rare species did not become a common species. The total environment is important for the species composition of the mosquito fauna; this composition will change if the environment changes, as in the study area during the last 30 years. If a similar study were to be undertaken in ten years time, the results might be very different.

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APPENDIX 1

Key to the fourth instar larvae and adult female mosquitoes at Flatbush, Alberta

Key to the Genera of Larvae

1. Air tube present 2

   Air tube absent .... *Anopheles*

2. Air tube short, apex adapted for piercing the roots of aquatic plants .... *Mansonia*

   Air tube long, adapted for penetrating the surface water film 3

3. Siphonal tufts at base of air tube; lower tufts of dorsal brush each a branched hair ...... *Culiseta*

   Siphon without a pair of basal siphonal tufts; siphonal tufts some distance from the base, usually beyond pecten 4

4. One pair of ventral siphonal tufts usually situated beyond pecten; if more than one pair of tufts the additional ones are found laterally and dorsally on air tube; anal segment not ringed by dorsal plate (except *A. punctor*) .... *Aedes*

   Several pairs of ventral siphonal tufts; anal segment ringed by dorsal plate .... *Culex*

The following genera are represented by only one species each:

Genus ANOPHELES Meigen

Anopheles earlei Vargas

Genus CULEX Linnaeus

Culex territans (Walker)

Genus MANSONIA Blanchard

Mansonia perturbans (Walker)

Key to the fourth instar CULISETA larvae

1. Air tube with normal pecten teeth on basal fourth not followed by long hairs; antennae longer than head .... *morsitans*

   Air tube with normal pecten teeth near base followed by a series of long hairs extending beyond the middle of air tube; antennae shorter than head 2

2. Upper and lower head hairs with similar number of branches .... *impatiens*

   Upper head hairs seven to ten branches; lower head hairs three to five branches 3

3. None or only one tuft pierces the sclerotised plate of ninth segment; antennae not prominently spined 4

   Three tufts pierce the sclerotised plate; antennae prominently spined .... *alaskaensis*

4. Basal pecten teeth simple or with one or two small appressed denticles .... *incidens*

   Basal pecten teeth flattened with three or four appressed denticles .... *inornata*

Key to fourth instar AEDES larvae

1. Anal segment completely ringed by anal plate .. punctor

Anal segment not completely ringed by anal plate 2

2. Antennae shorter than head 3

Antennae longer than head; last two teeth of pecten widely spaced; head hairs usually triple .... diantaeus

3. Pecten with evenly spaced teeth usually not extending beyond middle of siphon 4

Pecten with one or more widely spaced distal teeth often extending beyond the middle of the siphon 9

4. Upper and lower frontal head hairs multiple 5

Upper and lower frontal head hairs with less than three branches 7

5. Air tube more than four times as long as wide; scales on eighth segment with prominent median spine; prothoracic hairs 1 and 5 long and triple .... fitchii

Air tube approximately three times as long as wide .. 6

6. Prothoracic hairs 1 and 5 both single ...... canadensis

Prothoracic hair 1 single, hair 5 triple ...... pionips

7. Upper and/or lower head hairs single................. 8

Lower head hairs double, upper triple; prothoracic hairs 1 and 5 single .... sticticus

8. Scale of lateral comb of eighth segment flattened and apically fringed; one tuft of ventral brush

8.(cont) precedes barred area .... communis

Scale of lateral comb pointed, median spine longer than lateral ones; 3 or 4 tufts of ventral brush precedes barred area ...... implicatus

9. Pecten extending well beyond the insertion of the siphonal tuft 10

Pecten ending at or before the insertion of the siphonal tuft 11

10. Last four pecten teeth well separated distally; air tube with ventral tuft only; head hairs single .... cataphylla

Last 5 pecten teeth well separated distally; air tube with 4 dorsal and 2 lateral tufts in addition to the ventral tuft .... trichurus

11. Last 3 pecten teeth well separated distally 12

Fewer than last 3 pecten teeth well separated distally 13

12. Ventral tuft beyond last pecten tooth; siphonal index 4; comb scales pointed with small fringing points; upper and lower head hairs double .. riparius

Ventral tuft not beyond last pecten tooth; siphonal index 3; comb scales not pointed with no side points; upper and lower head hairs triple or multiple .... intrudens

13. Comb of eighth segment a triangular patch 14

Comb of eighth segment an irregular double row 15

14. Last pecten tooth slightly detached; prothoracic hairs 1 and 5 double; head hairs multiple ...flavescens

14.(cont) Last 2 pecten teeth detached; prothoracic hairs 1 and 5 single; head hairs double .... *excrucians*

15. Head hairs single .... *spencerii*

Head hairs triple or multiple 16

16. Last 2 pecten teeth well separated; scale comb a long single spine; lower head hairs double, upper multiple .... *vexans*

All pecten teeth spread out; comb scales pointed, each point with small accessory points; head hairs multiple .... *cinereus*

Key to the Genera of female Mosquitoes

1. Scuttelum rounded; palpi of female over half as long as proboscis; abdomen without scales..*Anopheles*

Scuttelum trilobed; palpi less than one half as long as proboscis; abdomen with scales 2

2. Spiracular bristles present; postspiracular bristles absent; tip of abdomen rounded .... *Culiseta*

Spiracular bristles absent 3

3. Postspiracular bristles present 4

Postspiracular bristles absent, tip of abdomen blunt .... *Culex*

4. Wing scales very broad; tip of abdomen blunt.. *Mansonia*

Wing scales narrow, tip of abdomen pointed ...... *Aedes*

The following genera are represented by only one species:

Genus ANOPHELES Meigen

Anopheles earlei Vargas

Genus CULEX Linnaeus

Culex territans (Walker)

Genus MANSONIA Blanchard

Mansonia perturbans (Walker)

Key to female CULISETA Mosquitoes

1. Tarsi with narrow or wide rings of white scales on some or all the segments 2

   Tarsi without rings of white scales 4

2. Wings without conspicuous spots of dark scales; tarsal rings narrow .... _morsitans_

   Wing scales form dense spots on some veins; tarsal rings narrow or wide 3

3. Hind tarsi with narrow white rings; wing scales form long spots on radial vein ..... _incidens_

   Hind tarsi with wide white rings; wing scales form dense spots; a very large species .... _alaskaensis_

4. Abdominal tergites with numerous white scales, widening laterally to cover most of the segment; numerous white scales on costa and subcosta .... _inornata_

   Abdominal tergites with narrow even basal bands; wings dark scaled .... _impatiens_

Key to female AEDES Mosquitoes

1. Tarsal segments ringed with white 2

   Tarsal segments not ringed with white 7

2. White rings basal and apical .... canadensis

White rings basal only 3

3. Basal white bands of tarsal segments very narrow; lower mesepimeral bristles present; abdominal segments with white kidney shaped markings and metallic coloured scales .... vexans

Basal white bands broad 4

4. Large yellow - white species; abdominal segments completely covered by yellow scales; many white wing scales .... flavescens

Abdominal tergites with abundant dark scales 5

5. Tarsal claw very large, main claw almost parallel with tooth (Key Fig. 1) .... excrucians

Tarsal claw smaller, not sharply bent, tooth small 6

6. Mesonotum uniformly brown; no mesepimeral bristles; tarsal claw as in Key Fig. 2 .... riparius

Sides of mesonotum greyish; lower mesepimeral bristles 1 or 2 or absent; tarsal claw as in Key Fig. 3 .... fitchii

7. Very small species; tergites with metallic gleam and (usually) no basal white bands; sternites white; fore coxa with a patch of brown scales on anterior surface .... cinereus

Tergites with white scales; fore coxa white scaled .. 8

8. Wing scales distinctly bicoloured, some veins with only white scales .... spencerii

Wing scales entirely dark, or with only a

8.(cont) patch of white scales restricted to base of costa 9

9. Post coxal scale patch present 10

Post coxal scale patch absent 14

10. Mesonotum with scales along lateral edge silver-grey; median lines largely pale brown, broad, poorly defined; base of costa with a distinct patch of white scales; bristles of scuttelum black 11

Mesonotum with scales along lateral margin yellow or dark, not silver-grey; median lines usually narrow and well defined; rarely any white scales at base of costa 13

11. Basal seventh of costa white scaled; veins C, Sc, and R with a few white scales; tibia and basitarsi anteriorly with many white scales .... _cataphylla_

White scales restricted to extreme base of costa; tibia and basitarsi anteriorly with few, if any, white scales 12

12. Sternopleuron with scales extending about half way to anterior angle; brown median stripe distinct .... _implicatus_

Sternopleuron with scales extending to anterior angle; median stripe indistinct, the scutum appearing 'frosted' .... _trichurus_

13. Bristles of scuttelum and mesonotum all black; mesonotal stripes black, separated medially

13. (cont) by a thin yellow line; many white scales on probasisternum .... _pionips_

Bristles of scuttelum and mesonotum yellow or bronze; sharply defined brown mesonotum band; white triangular abdominal bands ..... _punctor_

14. Mesonotum uniform bronze or with very faint indications of median lines; sometimes a small, patch of white scales at base of costa; torus yellow; scales of sternopleuron not extending to anterior angle (cf. _A. communis_) .... _intrudens_

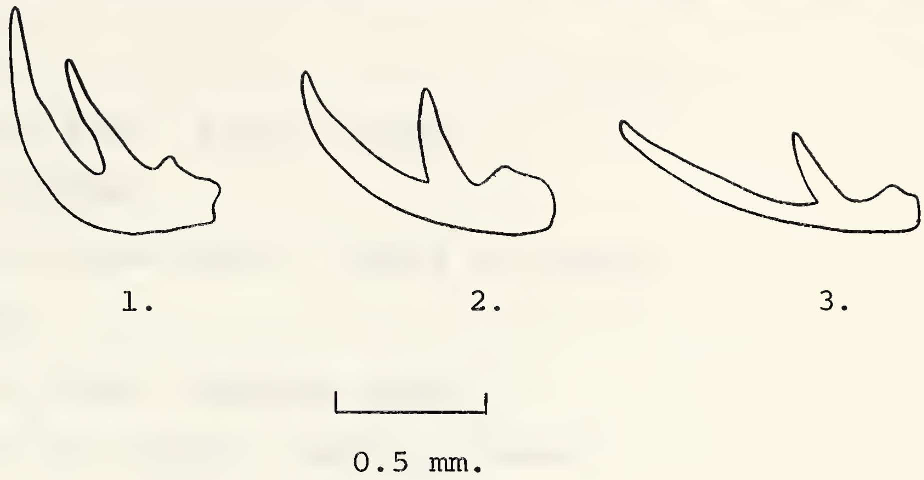
Mesonotum with distinct line(s) contrasting in colour with marginal scales 15

15. Basal white abdominal bands distinct; bristles of scuttelum and mesonotum black or dark 16

Basal white bands indistinct or lacking; bristles of scuttelum and mesonotum yellow .... _diantaeus_

16. Mesonotal pattern not well defined; sides of mesonotum yellow or brown; lower mesepimeral bristles present; scales of sternopleuron extending to anterior angle .... _communis_

Mesonotal stripe wide and brown; sides of mesonotum yellow-white; mesepimeral bristles absent .... _sticticus_



Key Figs. 1 - 3. 1, tarsal claw of *A. excrucians*;
2, tarsal claw of *A. fitchii*;
3, tarsal claw of *A. riparius*.

APPENDIX 2

Mammals seen at Flatbush, Alberta: Summer 1961 and 1962

SORICIDAE

Masked Shrew *Sorex cinereus*

VESPERTILIONIDAE

Little Brown Myotis *Myotis lucifugus*

MUSTELIDAE

Least Weasel *Mustela rixosa*

Short-tail Weasel *Mustela erminea*

CANIDAE

Coyote *Canis latrans*

FELIDAE

Lynx *Lynx canadensis*

SCIURIDAE

Woodchuck *Marmota monax*

Richardson Ground Squirrel *Citellus richardsonii*

Least Chipmunk *Eutamias minimus*

Thirteen-lined Ground Squirrel *Citellus tridecemlineatus*

Red Squirrel *Tamiasciurus hudsonicus*

Northern Flying Squirrel *Glaucomys sabrinus*

CASTORIDAE

Beaver *Castor canadensis*

CRICETIDAE

Deer Mouse *Peromyscus maniculatus*

Boreal Redback Vole *Clethrionomys gapperi*

Meadow Vole *Microtus pennsylvanicus*

Muskrat *Ondatra zibethica*

MURIDAE

House Mouse *Mus musculus*

ZAPODIDAE

Meadow Jumping Mouse *Zapus hudsonicus*

ERETHIZONTIDAE

Porcupine *Erethizon dorsatum*

LEPORIDAE

Snowshoe Hare *Lepus americanus*

CERVIDAE

Mule Deer *Odocoileus hemionus*

Whitetail Deer *Odocoileus virginianus*

Moose *Alces americana*

Birds seen at Flatbush, Alberta: Summer 1961 and 1962

GAVIIDAE

Common Loon *Gavia immer*

COLYMBIDAE

Rednecked Grebe *Colymbus griegena holboelli*

Horned Grebe *Colymbus auritus*

ARDEIDAE

American Bittern *Botaurus lentiginosus*

ANATIDAE

Canada Goose *Branta canadensis*

Snow Goose *Chen hyperborea*

Mallard *Anas platyrhynchos platyrhynchos*

Pintail *Dafila acuta*

Green-winged Teal *Anas carolinense*

Blue-winged Teal *Anas discors*

ANATIDAE

Baldpate *Mareca americana*

Shoveller *Spatula clypeata*

Redhead *Aythya americana*

Ring-necked Duck *Aythya collaris*

Canvasback *Aythya valisneria*

Lesser Scaup *Aythya affinis*

American Goldeneye *Bucephala clangula*

Bufflehead *Bucephala albeola*

Old Squaw *Clangula hyemalis*

White winged Scoter *Melanitta deglandi*

Surf Scoter *Melanitta perspicillata*

American Merganser *Mergus merganser americanus*

Red-breasted Merganser *Mergus serrator*

ACCIPITRIIDAE

Goshawk *Accipiter gentilis atricapillus*

Sharp shinned Hawk *Accipiter striatus velox*

Red-tailed Hawk *Buteo jamaicensis borealis*

Marsh Hawk *Circus cyaneus hudsonius*

FALCONIDAE

Sparrow Hawk *Falco sparverius*

TETRAONIDAE

Spruce Grouse *Canachites canadensis*

Ruffed Grouse *Bonasa umbellus*

Sharp-tailed Grouse *Pedioecetes phasianellus*

Grey Partridge *Perdix perdix*

GRUIDAE

Sandhill Crane *Grus canadensis*

RALLIDAE

Virginia Rail _Rallus_ _limicola_ _limicola_

Sora Rail _Porzana_ _carolina_

Coot _Fulica_ _americana_

CHARADRIDAE

Killdeer _Charadrius_ _vociferus_

SCOLOPACIDAE

Wilson's Snipe _Capella_ _gallinago_ _delicata_

Upland Plover _Bartramia_ _longicauda_

Spotted Sandpiper _Actitis_ _macularia_

Greater Yellowlegs _Totanus_ _melanoleucus_

Lesser Yellowlegs _Totanus_ _flavipes_

Dowitcher _Limnodromus_ _griseus_

PHALAROPODIDAE

Wilson's Phalarope _Steganopus_ _tricolor_

LARIDAE

Herring Gull _Larus_ _argentatus_

California Gull _Larus_ _californicus_

Ring-billed Gull _Larus_ _delawarensis_

Franklin's Gull _Larus_ _pipixcan_

STERNIDAE

Black Tern _Chlidonias_ _nigra_ _surinamensis_

COLUMBIDAE

Western Mourning Dove _Zenaidura_ _macroura_ _marginella_

STRIGIDAE

Barred Owl _Strix_ _varia_

Horned Owl _Bubo_ _virginianus_

Short-eared Owl _Asio_ _flammeus_ _flammeus_

CAPRIMULGIDAE

Nighthawk *Chordeiles minor*

TROCHILIDAE

Ruby throated Hummingbird *Archilocus colubris*

ALCEDINIDAE

Belted Kingfisher *Megaceryle alcyon*

PICIDAE

Yellow-shafted Flicker *Colaptes auratus borealis*

Pileated Woodpecker *Dryocopus pileatus*

Yellow-bellied Sapsucker *Sphyrapicus varius*

Hairy Woodpecker *Dendrocopus villosus*

Downy Woodpecker *Dendrocopus pubescens*

TYRANNIDAE

Eastern Kingbird *Tyrannus tyrannus*

Eastern Phoebe *Sayornis phoebe*

Say's Phoebe *Sayornis saya saya*

Least Flycatcher *Empidonax minimus*

HIRUNDINIDAE

Tree Swallow *Iridoprocne bicolor*

Bank Swallow *Riparia riparia riparia*

Cliff Swallow *Petrochelidon pyrrhonota*

CORVIDAE

Canada Jay *Perisoreus canadensis*

Blue Jay *Cyanocitta cristata*

American Magpie *Pica pica hudsonia*

Crow *Corvus brachyrhynchos*

PARIDAE

Black-capped Chickadee *Parus atricapillus*

PARIDAE

Boreal Chickadee _Parus hudsonicus_

SITTIDAE

Red-breasted Nuthatch _Sitta canadensis_

CERTHIDAE

Brown Creeper _Certhia familiaris_

TURDIDAE

Robin _Turdus migratorius_

Hermit Thrush _Hylocichla guttata_

BOMBYCILLIDAE

Cedar Waxwing _Bombycilla cedrorum_

STURNIDAE

Starling _Sturnus vulgaris_

VIREONIDAE

Solitary Vireo _Vireo solitarius_

Red-eyed Vireo _Vireo olivaceus_

Warbling Vireo _Vireo gilvus swainsoni_

COMPSOTHLYPIDAE

Tennessee Warbler _Vermivora perigrina_

Yellow Warbler _Dendroica petechia_

Myrtle Warbler _Dendroica coronata_

Ovenbird _Seirus aurocapillus_

Canada Warbler _Wilsonia canadensis_

American Redstart _Setophaga ruticilla_

PLOCEIDAE

House Sparrow _Passer domesticus domesticus_

ICTERIDAE

Red-winged Blackbird _Agelaius phoeniceus_

ICTERIDAE

Baltimore Oriole *Icterus galbula*

Brewer's Blackbird *Euphagus cyanocephalus*

Common Grackle *Quiscalus quiscala*

Common Cowbird *Molothrus ater*

THRAUPIDAE

Western Tanager *Piranga ludoviciana*

FRINGILLIDAE

Evening Grosbeak *Hesperiphona vespertina*

Rose-breasted Grosbeak *Pheucticus ludovicianus*

Purple Finch *Carpodacus purpureus*

Pine Siskin *Spinus pinus pinus*

Slate colored Junco *Junco hyemalis hyemalis*

Tree Sparrow *Spizella arborea ochracea*

Chipping Sparrow *Spizella passerina*

White-crowned Sparrow *Zonotrichia leucophrys*

White-throated Sparrow *Zonotrichia albicollis*

Fox Sparrow *Passerella iliaca*

Song Sparrow *Melospiza melodia*

Amphibians seen at Flatbush, Alberta: Summer 1961 and 1962

BUFONIDAE

Dakota Toad *Bufo hemiophrys*

RANIDAE

Wood Frog *Rana sylvatica*

Burt and Grossenheider (1952) was used to identify the mammals; Peterson (1961) to identify the birds; and Blair *et al.* (1957) to identify the amphibians.